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Abundance of the coastal morphotype of bottlenose dolphin, *Tursiops truncatus*, in U.S. continental shelf waters between New Jersey and Florida during winter and summer 2002.

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Executive Summary

Bottlenose dolphins in coastal waters of the US Atlantic continental shelf are currently defined as depleted under the Marine Mammal Protection Act and are the focus of a Take Reduction Team process to reduce incidental mortality due to commercial fisheries activities. The benchmark defining the level of human-induced mortality that will still allow recovery of the population is potential biological removal (PBR). A key component of the PBR calculation is the minimum population estimate for a given stock which is derived from absolute abundance estimates and associated levels of uncertainty.

There are two distinct morphotypes of bottlenose dolphin, and the "coastal" morphotype occurring in nearshore waters is the focus of the current management action. In some areas of the coast, the coastal and "offshore" morphotypes have overlapping spatial distribution. The two forms cannot be distinguished visually during aerial abundance surveys, and this has complicated efforts to assess the abundance of the coastal morphotype of bottlenose dolphins.

In this document, we develop an updated abundance estimate for bottlenose dolphins using results from surveys conducted during summer and winter 2002. We have used an analysis of spatial pattern and information from genetic analysis of tissue biopsy samples to evaluate the relative spatial distribution of the offshore and coastal morphotypes as a function of habitat variables and spatial location across the latitudinal range. These models of relative distribution were combined with abundance survey data to develop an abundance estimate for the coastal morphotype alone.

There are seven identified seasonal management units for the coastal morphotype of bottlenose dolphins from New Jersey to central Florida (Figure 1). The current analysis focuses only on the abundance of animals in coastal waters between depths of 0-40m, and excludes estuarine areas where there may be either distinct estuarine stocks or where animals belonging to the coastal stocks may occur. Separate abundance estimates for each of the seven coastal management units were derived for summer and winter.

The analytical methods used to develop abundance estimates for coastal morphotype bottlenose dolphins are described in detail in this document. Based upon these analyses, the derived abundance estimates for each management unit are given below.

Table i: Mean total estimated abundance of the coastal morphotype of bottlenose dolphins between 0-40 m depth by management unit during summer 2002. Estimates are for 0-20 m depth in the central and northern Florida units. (Repeated as Table 33 in text).

Management Unit	Mean Abundance	SE Abundance	% CV	95 % Confidence Interval	Lower Limit 60% CI (Nmin)
Northern Migratory	17466.1	3334.3	19.1	11497.7 – 24956.5	14620.9
N. North Carolina	6160.2	3197.9	51.9	1484.9 – 13399.0	3254.7
S. North Carolina	3645.8	4048.0	111.0	1084.1 – 13135.6	1863.2
South Carolina	2283.5	627.2	27.5	1160.1 – 3701.0	1776.4
Georgia	6234.8	3151.4	50.5	2089.8 – 13388.7	3335.4
Northern Florida	736.6	346.3	47.0	345.1 – 1585.3	454.9
Central Florida	718.4	365.3	50.9	148.7 – 1561.9	402.9

Table ii: Mean total estimated abundance of the coastal morphotype of bottlenose dolphins between 0-40 m depth by management unit during winter 2002. Estimates are for 0-20 m depth in the Georgia management unit. (Repeated as Table 38 in text).

Management Unit	Mean Abundance	SE Abundance	% CV	95 % Confidence Interval	Lower Limit 60% CI (Nmin)
North Carolina	16913	3887.1	23.0	10230.3 –25512.5	13558.4
South Carolina	2378.3	715.0	30.1	1348.0 – 4284.4	1815.8
Georgia	2012.5	670.1	33.3	925.0 – 3471.9	1497.1

These estimates account for several sources of bias and include a correction for perception bias. However, they do not account for availability bias during the survey. Since group sizes were large during both surveys and bottlenose dolphins have relatively short dive intervals, it is expected that the magnitude of this negative bias is relatively small.

The greatest source of potential bias (positive or negative) in these estimates is the models describing the distribution of the coastal morphotype. Sample sizes were generally small, particularly during winter months and may not be representative of the entire survey range due to limits on the geographic range of collected biopsy samples. Additional biopsy sampling and genetic analysis are required to improve the robustness of these models and reduce both uncertainty and bias in the resulting abundance estimates.

The results presented here can be combined with abundance data from estuarine waters, where appropriate, to estimate minimum population size and revised PBR values for the coastal morphotype of bottlenose dolphins on the U.S. Atlantic coast.

I. Introduction and Summary of Previous Assessments

The bottlenose dolphin, *Tursiops truncatus*, is a common species encountered in estuaries, coastal waters, and continental shelf waters of the U.S. Atlantic. During 1987-1988, a major die-off attributed to an epizootic event occurred coastwide resulting in high numbers of stranded animals. This mortality event was estimated to decrease the population size by approximately 53% (Scott *et al.*, 1988); however, a more recent analysis of these data suggests that the actual decline may have been only 10-27% of pre-1987 population levels assuming a single coastal stock (Eguchi, 2002).

Spatial and temporal patterns in stranding rates during the 1987-1988 mortality event were used to infer stock structure. The frequency of strandings showed a distinct seasonal trend with high numbers of strandings north of Cape Hatteras, NC, during the summer and progressing south of Cape Hatteras during the winter. Based upon these patterns, Scott *et al.* (1988) hypothesized a single coastal migratory stock occurring from New Jersey to Cape Hatteras during summer and moving south of Cape Hatteras and ranging as far south as central Florida during the winter. Based upon the apparent reduction in population size during the 1987-1988 die-off, the western North Atlantic coastal bottlenose dolphin stock was classified as depleted under Marine Mammal Protection Act (MMPA) guidelines in 1993. There are numerous estuarine sites in the southern part of the range with known resident animals (e.g., Zolman, 1996; Petricig, 1995; Odell and Asper, 1990) that were not considered to be part of this coastal stock.

More recent analyses have demonstrated that there are in fact multiple genetically and/or behaviorally distinct stocks of bottlenose dolphin in coastal waters of the US Atlantic. Based upon genetics, stable isotope analysis of tissues, photo-identification records, and satellite tag telemetry data, seven seasonal management units have been described within distinct latitudinal ranges along the coastline (NMFS, 2001; Figure 1). During winter months, the northern migratory management unit moves south and overlaps with the southern North Carolina and northern North Carolina units. These three overlapping stocks are collectively referred to as the winter North Carolina management units. The seven management units replace the previously defined single coastal migratory stock. Many of the management unit boundaries are tentative at

this point, and continued refinement of the latitudinal stock structure within coastal waters is an active area of research. In addition, the extent to which estuarine animals utilize coastal habitats remains unclear. It is probable that there is additional population structure along the US Atlantic coast that is not incorporated in the current management units (NMFS, 2001).

In addition to the complexity in latitudinal stock structure, there are two distinct morphotypes occurring in US Atlantic waters described as the "coastal" and "offshore" forms of bottlenose dolphin. The two morphotypes can be distinguished based upon differences in morphometrics, blood chemistry and feeding habits (Duffield, 1986; Hersh and Duffield, 1990; Mead and Potter, 1995). The two forms are genetically distinct based upon both mtDNA and nuclear markers (Hoelzel *et al.* 1998), and individual animals can be positively identified to a particular morphotype from tissue samples and genetic analysis (P. Rosel, unpublished data). Animals can often be distinguished visually during close encounter on shipboard and small vessel surveys; however, they cannot be distinguished during the aerial surveys used to determine population size. Analysis of the spatial distribution of the coastal and offshore morphotypes based on genetic samples collected in coastal U.S. waters indicated spatial overlap between the two morphotypes, particularly in waters between 6-81 km from shore south of Cape Hatteras during summer months (Torres *et al.*, in press). However, limited sample sizes in the region of overlap precluded accurate definition of appropriate habitat boundaries.

Previous analyses have used spatial patterns in survey data to infer stock boundaries between the coastal and offshore morphotypes. North of Cape Hatteras, there was a gap in sighting frequency during aerial surveys conducted in summer months during 1978-1982. Dolphin abundance was high in coastal waters <25 m depth, there was a region of very low abundance between 25-50 m depth, and an area of high abundance in waters deeper than 50 m near the continental shelf break (CETAP, 1982; Kenney, 1990). Based upon this pattern, the habitat boundary for the coastal migratory stock (i.e., coastal morphotype) was inferred to be the 25 m isobath. Aerial surveys conducted south of Cape Hatteras during the winter months did not indicate a clear spatial separation between the two morphotypes (Blaylock & Hoggard 1994).

In 1995, aerial surveys were conducted south of Cape Hatteras during winter and north of Cape Hatteras during the summer with the goal of assessing the abundance of the seasonally migrating coastal migratory stock. Spatial analyses were again used to identify longitudinal separation between the two morphotypes. A spatial boundary of 27 km from shore was inferred for the region south of Cape Hatteras during winter and a boundary of 12 km from shore was inferred for the region north of Cape Hatteras during summer. All animals within these boundaries were assumed to be of the coastal morphotype for the purpose of developing abundance estimates (Garrison, 2001). These inferred boundaries were considered provisional pending additional collection of tissue samples and analysis of genetic data to better describe the degree of spatial overlap.

The MMPA mandates that stock status be determined for marine mammal stocks that experience significant mortality due to human activities, in particular commercial fishing. Coastal morphotype bottlenose dolphins experience mortality related to fishing activities in coastal waters along the Atlantic coast. During 1997-1999, 995 bottlenose dolphins were observed to have stranded along the Atlantic coast, and approximately 50% of fresh carcasses could be positively associated with signs of fishery interactions such as entanglement in fishing lines, net marks, etc. (Waring *et al.*, 2002). In observed mid-Atlantic gillnet fisheries, annual average mortality of the coastal morphotype of bottlenose dolphin between 1996-2000 was estimated at 30 animals in the northern migratory management unit during summer, 23 animals in the northern North Carolina management unit during summer, and 180 animals in the winter North Carolina management unit (Palka and Rossman, 2001; Waring *et al.*, 2002). These estimated mortality rates exceed allowable levels under the MMPA. Under these conditions, the MMPA mandates that a Take Reduction Team consisting of relevant stakeholders (e.g., conservation groups, scientists, and fishing industry representatives) be convened to develop strategies to reduce bottlenose dolphin mortalities due to commercial fishing activities. The bottlenose dolphin take reduction team (BDTRT) was convened in November, 2001.

The primary benchmark used to guide management decisions under the MMPA is potential biological removal (PBR). This benchmark reflects the number of animals that can be removed from a marine mammal population and still allow recovery of a depleted stock or

maintenance of a stock at its optimum sustainable population (OSP) size. The quantity is based upon population simulations under a variety of assumptions and accounts for the reproductive rate of the stock, the current status relative to OSP, uncertainty in measures of mortality rates, and uncertainty in measures of abundance (Wade and Angliss, 1997). Calculation of PBR implicitly requires knowledge of stock structure and directly incorporates an estimate of abundance with appropriate quantification of uncertainty. The abundance term in the PBR formula is the minimum stock abundance (N_{min}), where N_{min} is taken as the lower bound of the 60th percentile confidence interval from a log-normally distributed estimate of absolute abundance (Wade and Angliss, 1997). At the time the BDTRT was convened, there were several weaknesses in the supporting data pertaining to calculation of PBR that were noted both in assessment documents and during peer review of those documents. These create uncertainty as to the actual value of PBR and include:

1) Uncertainty in the longitudinal boundaries separating the coastal and offshore morphotypes. During previous analyses of spatial pattern, there were no available data to explicitly quantify either the degree of mixing or the uncertainty in spatial boundaries used to define the coastal morphotype habitat. If the boundaries are defined incorrectly, then there will be some degree of either positive or negative bias in the abundance estimate and PBR. In addition, ignoring uncertainty in these boundaries results in a direct positive bias in PBR since the confidence bounds on the abundance estimates are too small (Garrison, 2001).

2) The abundance estimates included several potential sources of bias. The aerial surveys used to derive abundance estimates and PBR were conducted during winter and summer of 1995 and were designed based upon the concept of a single coastal migratory stock. As a result, the geographic range of these surveys did not fully correspond to the newly defined management units, and several management units were not fully covered by the survey. Second, no data was available to account for a known source of negative bias in visual line transect surveys of marine mammals termed "visibility bias". Standard line transect analyses assume that all animals on the trackline are seen by the survey team. If animals are beneath the surface or are missed by the observers this assumption is violated, and the resulting abundance estimate is negatively biased to an unknown degree (Buckland *et al.*, 1993). These potential sources of bias and uncertainty

were noted in the original assessment document (Garrison and Yeung, 2001) and in presentations to the TRT, but they could not be explicitly quantified and incorporated into the resulting PBR calculations.

During 2001 and 2002, SEFSC conducted several studies to address some of these issues. In summer 2001 and 2002, major sampling efforts were undertaken to collect tissue samples to better define the longitudinal boundaries between the coastal and offshore morphotypes. More localized biopsy sampling was also conducted during winter 2002. During winter and summer 2002, aerial surveys were conducted to provide improved estimates of abundance across the newly defined management units. These surveys included methods to account for visibility bias and provide more accurate abundance estimates for each management unit. The goal of the current document is to analyze the recent survey efforts and develop abundance estimates for the coastal morphotype bottlenose dolphin in continental shelf waters for each management unit with appropriate measures of uncertainty. The resulting estimates can be used in conjunction with available estimates for estuarine waters to update PBR levels and evaluate the effectiveness of proposed measures for reducing fishery mortalities to below PBR.

II. Analytical Strategy

The goal of the current analysis is to develop abundance estimates for coastal morphotype bottlenose dolphins in seasonal management units (Figure 1) during winter and summer 2002.

Four tasks are required to assess the abundance of coastal morphotype bottlenose dolphin, and each corresponds to following sections in this document:

1) Evaluate spatial distribution as a function of habitat variables across management units during summer and winter aerial surveys. This analysis described regional differences in the spatial patterns of bottlenose dolphins and determine if there are clear gaps in spatial distribution that may correspond to separation between the coastal and offshore morphotypes. Results from this analysis will be used primarily to group management units into larger regions with similar spatial patterns, and these regional differences will be included in the analysis of morphotype distribution based on genetic data.

2) Evaluate the spatial distribution of coastal vs. offshore morphotype bottlenose dolphins as a function of habitat characteristics based on genetic analysis of skin biopsy samples. Where there are no clear spatial patterns indicating habitat differences, it is necessary to take a probabilistic approach to predicting whether a bottlenose dolphin group observed at any spatial location is of the coastal morphotype. Since there is known mixing between the two morphotypes through at least some of the range, it is important to accurately quantify the uncertainty in this prediction to fully represent the uncertainty in derived abundance estimates. These analyses were conducted on a regional basis grouping management units based on the spatial analysis in step 1.

3) Estimate the total abundance of bottlenose dolphins (both coastal and offshore morphotype) in coastal continental shelf waters during summer and winter 2002 between New Jersey and Florida. Aerial survey effort was allocated among the various management units to provide both complete spatial coverage and sufficient precision in the abundance estimates to address the weaknesses identified during the 1995 surveys. In addition, the surveys included two independent observer teams on the aircraft to quantify a component of visibility bias and thereby reduce this known source of negative bias.

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4) Combine abundance estimates and models of coastal morphotype distribution developed in step 2 to generate seasonal abundance estimates for each management unit and quantify uncertainty. Both animal abundance and the morphotype identification have associated measures of uncertainty, and it is important to combine these to accurately represent the uncertainty in the resulting abundance estimates. As noted above, the value for PBR reflects both the absolute level of abundance and the degree of uncertainty in that estimate. Thus, it is important to develop an unbiased abundance estimate and to properly quantify the uncertainty.

III. Survey Design and Methodology

Aerial Visual Line Transect Surveys

Between 15 January and 28 February 2002, an aerial survey was conducted in Atlantic coastal waters to assess the abundance of bottlenose dolphins in waters between 0-40m depth. Approximately 7,500 km of survey effort was planned during 120 hours of flight time and 45 survey days. The survey was planned in two sets of replicate lines covering the region from the Cape Canaveral, FL (28.45°N) to the southern edge of Delaware Bay (38.80°N). The lines within each replicate were uniformly spaced from a random starting point. Line spacing was approximately 10 km apart; however, since the replicates were offset, line spacing typically ranged between 2-5 km. The first replicate covered the area between 0-20 m depth, while the second included waters from 0-40 m depth (Figure 2). Replicate 2 lines extending further offshore were only planned for the North Carolina and South Carolina regions due to limitations on survey effort. A total of 4,800 km of transect line was planned in the 0-20m depth stratum while 2,700 km were planned in the 20-40m depth range. The higher effort level in the coastal stratum reflects both higher sampling priority for this area and expected higher abundance. Transect lines south of the Georgia-Florida state line were not surveyed because survey time was lost due to weather. A total of 6,411 km of trackline was completed during the survey, and 185 bottlenose dolphin groups were sighted including 2,114 individual animals.

A complimentary survey was conducted between 15 July to 31 August, 2002. As with the winter survey, effort was stratified into 0-20 m and 20-40 m depth zones. Survey lines in the 0-20 m depth strata were spaced approximately 10 km apart, and lines extending to 40 m depth were spaced approximately 30 km apart (Figure 3). A total of 7,610 km of survey trackline was planned extending from Sandy Hook, NJ (Latitude 40.5 °N) to Ft. Pierce, FL (Latitude 27.3 °N). This included approximately 4,880 km of trackline in the 0-20 m stratum and 2,730 km of trackline in the 20-40 m depth stratum. All tracklines in the 0-20 m stratum, were completed throughout the survey range while offshore lines were completed only as far south as the Georgia-Florida state line. A total of 6,734 km of trackline were completed. A total of 185 bottlenose dolphin groups were sighted during the survey including 2,544 individual animals.

The surveys followed standard procedures for SEFSC and NOAA fisheries aerial sighting surveys and follow the design considerations for distance analysis of line transect survey data (Buckland *et al.*, 1993). The aircraft used during the survey was a NOAA DeHavilland DHC-6 Twin Otter. The survey crew consisted of 6 scientists occupying 5 sighting stations and a data recorder position. The aircraft was equipped with large Plexiglas bubble windows on either side in the forward part of the cabin that provided visual observers with forward, lateral, rear, and downward visibility. The bubble windows allowed the observer to view the area on the trackline directly beneath the aircraft. In the aft portion of the cabin, there were two smaller bubble windows that provided relatively limited visibility beneath the aircraft and a belly window position that allowed both direct visibility beneath the airplane and deployment of camera and infra-red thermometer equipment (Figure 4). Survey tracklines were flown at an altitude of 229 m and an airspeed of 185 km hr^{-1} (100 knots). Surveys were only flown during favorable weather conditions when sea states were <= 3 on the beaufort scale.

During survey effort, observers were stationed at each of the five viewing positions operating as two independent survey teams. The forward and aft teams were separated visually by a curtain in the cabin and were isolated on separate intercom positions. Observers searched for marine mammals and turtles from directly beneath the aircraft to a perpendicular distance of approximately 1500 m. On sighting a marine mammal group, the observer measured the angle of the sighting when the group was perpendicular to the trackline either using a digital inclinometer or marks on the windows placed at 10 degree intervals. Sighting angles were used to calculate the perpendicular distance from the trackline for a marine mammal group. The observer waited until the group was well aft of the aircraft before informing the pilots, recorder, and the other team to allow both teams an opportunity to view the group independently. On notification that a group had been sighted, the aircraft was circled to reacquire the group and make group size estimates and verify species identification.

Data acquisition and recording was accomplished using a laptop computer connected to the aircraft's GPS system. Time, position, speed, and heading were recorded automatically at 1 minute intervals. The data recorder entered information on sea state, weather, glare, and other conditions that may influence sighting probabilities as conditions change during the survey. Sea

surface temperature was measured using an infrared thermometer at 10 second intervals and recorded on a separate computer.

The survey design and the use of two independent teams followed the recommendations of Buckland *et al.* (1993) and design considerations appropriate for using distance analysis of line transect survey data for abundance estimation. Line transects were angled so as to be roughly perpendicular to the bathymetry gradient to provide a representative sampling of animal density across the survey area. The stratification scheme was designed based upon previous studies and the expectation of both higher densities and higher proportion of coastal morphotype dolphins in the 0-20 m depth strata. Effort was allocated so as to include sufficient survey effort within each management unit to achieve coefficients of variation (CV) between 20-30% for resulting abundance estimates. The highest survey priority was placed on those management units with high fishery mortality rates (i.e., northern migratory, northern North Carolina, and winter North Carolina units).

The two team methodology was used to address a component of visibility bias. In standard distance analysis employing a single survey team, it is assumed that the probability of seeing animals on the trackline, g(0), is equal to 1. Where this assumption fails, there is a direct negative bias introduced into the abundance estimates. Visibility bias can be separated into two somewhat independent components, availability bias and perception bias (Marsh & Sinclair 1989). Availability bias occurs when the animals can not be observed within the searched area; for example, if bird nests are obscured by vegetation or marine mammals are underwater. This type of bias is often accounted for by separate models of animal availability to the observer such as detailed models of observer search behavior and animal dive-surface intervals for marine mammals (Barlow, 1999). Perception bias results from animals that were available to be seen but were missed by the observers. Primary factors that influence perception bias include weather conditions, observer fatigue, and observer experience (Laake *et al.*, 1997). Perception bias can often be reduced with adequate training of observers, frequent rotation to avoid fatigue, and limiting survey effort to periods where viewing conditions are favorable.

Estimating visibility bias requires modification of standard line transect survey methods. In general, this involves the use of an additional team of observers stationed either on the same platform or a different platform from the primary observer team (Buckland *et al.* 1993). The analytical methods for two-team visual line transect surveys employ a combination of line-transect and mark-recapture approaches (MRLT, Borchers *et al.* 1998, Laake 1999). These methods treat observations by the two teams as a sight-resight event. In an analogy to mark-recapture approaches, the initial sighting of a group of animals is considered a marking event, and a subsequent sighting of the same group is a recapture event. The two-team method and the MRLT approach can be implemented either by employing teams on two separate platforms (e.g., two airplanes) or by two teams on the same platform. In both cases it is imperative that a sighting by one team does not influence the probability of a sighting by the second team. In the case of two platform surveys, if there is sufficient separation between the lead and trailing platform both the perception and availability components of visibility bias can be addressed. However, increasing the trailing distance between the platforms increases the uncertainty in identifying duplicate sightings. The duplicate sighting issue has been approached using likelihood models that account for animal movement, dive rates, and platform speed (Hiby 1999). Where the two-teams are on the same platform, identifying recaptures is less problematic, however the short difference in the observation interval reduces the ability to estimate availability bias. This is particularly the case for fast moving platforms such as aircraft. Both teams are essentially observing the same area at the same time, and animals are likely to be unavailable to both teams. Thus, the current survey design directly estimates perception biases, but does not fully account for availability bias in the derived abundance estimates. The analytical methods used to develop abundance estimates from the winter and summer aerial surveys are described in the following sections.

Biopsy Collection Surveys

Tissue biopsy collection for genetic analysis has most typically concentrated on relatively small-scale sampling in local areas. These collections are generally targeted toward identifying genetic stock structure. However, these types of data collections are not appropriate for inferring information about broad-scale spatial distribution since sampling is rarely representative. For the current study, the primary consideration was to representatively sample bottlenose dolphins

across a broad spatial scale to infer patterns in the distribution of the coastal and offshore morphotypes. Systematic surveys were conducted to representatively sample bottlenose dolphins in continental shelf waters during the summers of 1998, 1999, 2001, and 2002. In addition, smaller data collection efforts and one large vessel survey were conducted during winter 2002.

Biopsy collection is difficult and involves logistic constraints and unavoidable sampling biases. Many of these difficulties are exaggerated in coastal and offshore waters where there are relatively low densities of animals to sample. Tissue samples from dolphins are collected using either pole spears, crossbows, or modified rifles. For each type of sampling tool, a custom sampling head has been developed that takes a small cylinder of tissue when the projectile impacts the animal. The sampling heads are designed to penetrate only the exterior blubber and minimize potential injury to the animal. Pole spear sampling is more reliable, as it does not involve aiming and firing a projectile, but it relies on animals to approach and "bowride" a vessel for sample collection. Samples can be collected using either crossbow or rifle at longer range, but the projectile must be aimed carefully, and it must be recovered along with any tissue sample.

After collection, skin samples were stored on ice in the sampling head and then transferred to a solution of 20% DMSO and saturated NaCl. Sample handling in the field was as sterile as possible, and efforts were made to avoid cross-contamination by using clean sampling heads, wearing gloves, etc. Tissue samples were analyzed for mitochondrial and nuclear markers that are unique to each morphotype and can positively identify individual animals (P. Rosel, unpublished data).

The sampling methods rely to some extent on the animals being "cooperative", and this imparts some inherent bias in using biopsy samples to infer spatial distribution. In the case of large vessel surveys, animals must approach the vessel and bowride since these vessels are not maneuverable enough to actively pursue animals. In small vessel surveys, animals must be tolerant of close approaches, and their behavior must be predictable enough to allow the sampler to anticipate animals movements, aim, and fire safely. In either case, if one morphotype is easier

to sample than another in a particular location the result will be a bias in any inferred spatial pattern. This type of bias is largely unavoidable, though using small vessels that are capable of pursuing less cooperative animals reduces the level of bias.

Small vessels that are more appropriate platforms for pursuing animals and collecting samples are not the best platforms for finding animals. Small vessels do not have long range viewing platforms and usually cannot safely operate in offshore waters. Further, these vessels cannot stay on the water overnight or in poor weather conditions, imposing additional logistic constraints on their sampling capabilities. Several approaches were taken to taken to address these constraints and reduce the degree of sampling bias.

During the summers of 1998 and 1999 and the winter of 2002, large-vessel surveys of the Atlantic continental shelf and slope were conducted by SEFSC. The summer 1999 survey was conducted aboard the NOAA Ship Oregon II (52 m total length) while the 1998 and 2002 surveys were conducted using NOAA Ship Gordon Gunter (75 m length). The primary goal of these surveys was to conduct visual line transect surveys to estimate abundance of marine mammals in U.S. Atlantic waters. In each case a secondary priority of the surveys included the collection of biopsy samples from bottlenose dolphins and other species of interest. Both vessels have viewing platforms high above the waterline and are equipped with high powered binoculars providing several miles of visibility. Survey tracks were uniformly spaced in "double sawtooth" pattern focusing on the continental shelf and slope within the U.S. EEZ from southern Florida to Delaware Bay (Figure 5). Bowriding animals were sampled by pole spear on the Oregon II and by rifle on the Gordon Gunter owing to differences in bow configuration between the two vessels. Both vessels are limited to operating in waters deeper than 10 m, and the goals of these surveys resulted in relatively little effort within waters < 20 m depth where the majority of coastal morphotype bottlenose dolphins are expected to occur. A total of 108 biopsy samples from bottlenose dolphin were collected during the summer surveys and 19 samples were collected during the winter 2002 survey.

During July-August, 2001 an extensive systematic survey of the coastal continental shelf from northern Florida to Long Island, NY was undertaken. The sampling design was developed

to provide systematic coverage of two depth strata corresponding to previously defined habitat types. The coastal (<= 10 m depth) area was expected to be an area of relatively high density of animals almost exclusively of the coastal morphotype. The offshore area (10-50m water depth) was an area of lower density and was expected to contain both the offshore and coastal morphotypes. Small vessels (50- 60' length) were employed primarily in deeper waters and an 18' boat was employed in nearshore waters in some regions. Biopsy sampling of encountered bottlenose dolphins was primarily attempted by pole-spear of bowriding animals on the larger vessels and by crossbow or rifle on the small boat. Survey teams were deployed simultaneously in regions along the coast. Within each region, coastal and offshore strata were typically sampled by different vessels. Vessels followed uniformly spaced zigzag tracklines to representatively sample across the habitat (Figure 6). Observers aboard the vessels searched for bottlenose dolphins and other marine mammals, and on encountering animals they turned to pursue and sample groups. For the larger vessels, it was generally only possible to sample bowriding animals due to limited maneuverability; however, in some cases a small boat could be deployed from the vessel to pursue and sample animals by crossbow. A total of 6,736 km of trackline was covered during summer 2001, 94 bottlenose dolphin groups were encountered, and 55 tissue samples were collected and used in the current analysis.

The vessels used during summer 2001 were not efficient sampling platforms. While they were able to operate in both shallow and deep water, they were generally not maneuverable enough to reliably sample encountered bottlenose dolphin groups. The vast majority of the survey time was spent searching for dolphins, encounters were relatively rare, and the number of samples collected was relatively small given the large amount of effort. During summer 2002, a combined aerial and boat survey was implemented to improve sampling efficiency. Given limited resources, the spatial extent of the 2002 survey was smaller than that of the 2001 survey and focused on the northern and southern North Carolina management units. During this survey, a highly maneuverable 6 m rigid hull inflatable boat was used in areas relatively close to shore, while a 41-foot vessel was used to operate in waters further offshore. The 41-foot vessel was also equipped with a small boat that could be deployed quickly to pursue and sample encountered animals. In concert with these vessels, a spotter airplane was used to conduct rapid, large scale surveys of the sampling area. On spotting and identifying a bottlenose dolphin group,

the aircraft contacted the nearest vessel, informed them of the group's location, and assisted them in locating the dolphin group. The sampled region was divided into six operational areas, each with a coastal and offshore stratum covering the area out to 40 m depth (Figure 7). The aircraft conducted closely spaced zigzag transects east to west across the sampling regions while the vessels generally moved north to south. The small vessels were generally more efficient at sampling bottlenose dolphin groups, though some groups could not be approached and sampled by any method. A total of 49 biopsy tissue samples was collected from bottlenose dolphins during this survey.

During winter, the logistic considerations of mounting large-scale survey efforts are complicated by uncertain weather conditions on the Atlantic coast. Biopsy sampling from small vessels require relatively calm seas (winds < 12 knots), and these types of days are uncommon during winter months. As a result, small, local sampling efforts have been used to provide information on spatial pattern during winter months. In general, these surveys made some attempt to representatively sample across the habitat range; however, operational constraints precluded systematic designs such as those used in the summer surveys. Local sample collections were conducted between late October 2001 and February 2002 in coastal waters of Georgia, south of Cape Fear, NC, and south of Cape Lookout, NC. A total of 125 biopsy samples collected in these efforts were included in the current analysis (Figure 8).

IV. Spatial Distribution During Aerial Surveys

Objective

In this analysis, we evaluate the relationships between the spatial distribution of bottlenose dolphins and habitat characteristics during the winter and summer 2002 aerial surveys. The primary goal is to determine whether or not there are clearly identifiable spatial patterns that indicate separation between the coastal and offshore morphotypes. The analysis will identify regional patterns of spatial distribution in an effort to identify management units that may be reasonably grouped together for the purposes of assessing the distribution of coastal vs. offshore morphotype animals using genetic data. The general approach is to use generalized additive models (GAM) to evaluate the relationship between bottlenose dolphin group density and habitat variables within spatial cells sampled during the aerial surveys. Separate GAM analyses were conducted for each management unit to evaluate regional differences in spatial patterns.

Methods

Statistical Modeling

Generalized additive models (GAM) are a flexible approach to exploring relationships between explanatory and response variables (Hastie and Tibshirani, 1990). In contrast to the more familiar generalized linear models (e.g., linear regression), GAMs do not assume any particular functional relationship between the explanatory and response variables, and instead use "smooth functions" to fit more complex curves whose shape is determined by the observed data. A number of smooth curve types can be fit to the observed data; however, for this application we have employed natural cubic splines because of the ability to specify the degrees of freedom and therefore the degree of smoothing of the data (Hastie and Tibshirani, 1990). The basic form of the GAM model is:

$$(1) \qquad y = \theta_0 + \sum_i f(x_i)$$

where y is the response variable, $f(x_i)$ represents the smooth functions for each of i explanatory variables, and θ_0 is an intercept term. Due to its flexibility, the GAM approach is increasingly

being applied to ecological problems including spatial patterns in fish trawl catches (Swartzman *et al.*, 1992), factors effecting sighting probabilities for marine mammals during visual surveys (Forney, 2000), and spatial models of cetacean abundance based on visual survey data (Hedley *et al.*, 1999).

As with linear models, the GAM can take a range of functional forms (i.e., link function) and variance structures as appropriate for the expected statistical distribution of the data. In the case of counts of items within spatial cells, a Poisson distribution is appropriate as the response can take effectively any value from 0 to ∞. For these data types, a log-linear link function with Poisson error structure is an appropriate model for the number of events observed as a function of explanatory variables (McCullagh and Nelder, 1989), and the form of the GAM function is:

$$(2) \qquad \log(N_k) = \log(E_k) + \theta_o + \sum_i f(x_{ik}),$$

where N_k is the expected count in a particular spatial cell k. The variable E_k is treated as an "offset" variable whose regression coefficient is equal to one, and it is appropriate where counts are standardized by some unit such as a time or area interval (McCullagh and Nelder, 1989).

A Poisson error structure is assumed in this model, and therefore the expected value of the variance is equal to the mean. However, in most cases in spatial data there will be some degree of autocorrelation that results in deviation from this expectation and generally "overdispersion" where the true variance is greater than that estimated by the Poisson model (McCullagh and Nelder, 1989). Model fitting procedures in GAMs are generally accomplished by iteratively evaluating the deviance of the model, a quantity that is not sensitive to departures from assumptions about the variance structure. However, the calculation of standard errors around predicted values, and inferences about differences in predictions between two models will be unreliable. Alternative non-parametric methods for variance estimation are therefore appropriate in the case of autocorrelated spatial data (e.g., Hedley *et al.*, 1999).

The approach used in the current study closely follows that described by Hedley *et al.* (1999). However, the goal of this study is not to develop a spatial model of absolute abundance but rather models of relative abundance as a function of habitat characteristics across the survey

area. The response variable is most appropriately described as "sightings per unit effort" (SPUE) or the number of dolphin groups observed per km of survey trackline within a particular spatial location. The assumption that sighting probability is independent of the spatial location and habitat variables across the survey area is implicit in this analysis.

Dolphin groups, as opposed to individual animals, are the appropriate unit of observation as groups of dolphins are expected to respond collectively to environmental variables rather than having separate responses for individual animals. Spatial patterns in SPUE measured as counts of groups may be expected to be different from those measured as counts of individuals if there is strong spatial pattern in group size as a function of spatial location or habitat variables. The relationships between group size and the habitat variables were explored by linear regression. As group sizes had an approximately log-normal distribution, regressions were performed on the log-transformed group sizes for each management unit.

Assigning Spatial Data

Survey tracklines from the summer and winter 2002 were assigned to 2 x 2 km spatial grid cells, and the total amount of survey effort (km) within each cell was calculated and used as the offset variable, E_k, in equation 2. A spatial resolution of 2 km was chosen to match the resolution of bathymetry and temperature data used as explanatory variables and to provide sufficient effort within cells to have a reasonable number of nonzero counts. The total number of dolphin groups observed within each spatial cell, N_k, is the response variable in this analysis.

The explanatory variables included two environmental variables and a spatial variable. Depth and sea surface temperature (SST) are habitat variables that are expected to influence the spatial distribution of dolphins both by influencing the distribution of their prey and exceeding thermal tolerances in the case of temperature. Bathymetry data for the continental shelf was obtained from published grids available from the National Geophysical Data Center (NGDC) that has produced 3-arc second resolution bathymetry data for the U.S. continental shelf (NGDC Coastal Relief Model, http://www.ngdc.noaa.gov/mgg/coastal). The average depth value within each spatial cell calculated from the appropriate bathymetry grid was used as the explanatory variable in the GAM.

SST data were collected using a belly mounted infrared (IR) thermometer during the aerial survey. However, on many days the thermometer did not operate properly, resulting in large spatial gaps in the available temperature data. SST data was obtained from satellite imagery from AVHRR sensors aboard NOAA polar orbiting environmental satellites (POES). The processed imagery from the region of interest is distributed through the Southeast Regional Node of the NOAA CoastWatch program (http://www.ccfhrb.noaa.gov). There are expected differences between satellite measured SST values and those from the aircraft sensor. Since the aircraft sensor failed over relatively large spatial regions, supplementing the SST data in these areas with satellite data and using IR sensor data in other areas would introduce a spatial bias. Therefore, SST data was derived from satellite imagery throughout the study region. Where possible, SST values from the satellite images were verified against IR sensor data. Spatially averaged satellite data was typically within 0.5 °C of IR sensor data where they were available for the same locations and days.

Processed satellite imagery for each day of the survey window was downloaded from the CoastWatch website. The images were then screened to find cloud-free images, and the best images matching each day's survey effort were identified and corrected for small variations in the spatial coverage ("geo-referenced"). Night-time satellite passes processed by combining multiple AVHRR channels ("split-window" processing) were most typically used and had the greatest consistency with IR measured temperature data. The nominal resolution of the regional images available from CoastWatch is 1.4 x 1.4 km. As with bathymetry data, the average of temperature values within each 2 km spatial cell was used as the explanatory variable.

Both depth and temperature are highly correlated with each other and are correlated with onshore to offshore gradients away from the coastline. Partitioning among these variables and identifying causal relationships between habitat variables and spatial distribution of dolphins is problematic, particularly when using only one year of data where no interannual variability in temperature patterns is included in the analysis. To account for the mutual correlation with spatial location, distance from shore (DFS) was included as a spatial variable. DFS was calculated using tools in ARCVIEW GIS (ESRI, Inc.). A grid of DFS for spatial locations in the

coastal habitat was developed by calculating the nearest distance from a high resolution coverage of the U.S. coastline using ARCVIEW Spatial Analyst software. All distance calculations were made in a Universal Transverse Mercator (UTM-83, Zone 18N) projection. The distance from shore for the center of each 2 km effort cell was used as the DFS explanatory variable in the GAM analyses.

Model Fitting and Evaluation

Model fit in GAM analysis is accomplished by examining patterns in the residual deviance and evaluating changes in explanatory power by comparison of deviance among various models (Hastie and Tibshirani, 1990). In addition, patterns of residuals are evaluated to identify non-linearity that may indicate important interaction effects and/or "overfitting" of the model. Due to the flexibility of the smooth functions, it is possible to fit spurious patterns in the data. Overfitting the model is avoided generally by selecting the most parsimonious model (Hastie and Tibshirani, 1990). In the current approach, smooth functions of each variable (depth, temperature, and DFS) were individually fit, and the deviance of these models was compared to the null model with only an intercept term to determine which individual factor(s) provided statistically significant explanatory power. Then, two term models with the most important variable and additional terms were fit to evaluate whether the subsequent variables provided additional explanatory power. Typically, the addition of a second model term did not provide additional explanatory power, and this is likely due to the high correlation between all three variables. Natural cubic splines with three degrees of freedom were used for all smooth functions, and model fit was not sensitive to the number of degrees of freedom included in this term. In some cases, linear terms were investigated and selected where patterns in the residuals indicated that the linear model was more appropriate than the smooth function.

Following selection of the model terms, predicted values of SPUE (groups km^{-1} effort) were generated along with analytical standard errors for these values. However, as noted above, spatially correlated data are likely to suffer from overdispersion of the Poisson error structure. In addition, the 2 km spatial cells cannot be considered independent sampling units in the survey design. The appropriate sampling unit for line transect surveys is the transect, and there is thus dependence among spatial cells on the same trackline. The standard error of predicted values is

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most likely underestimated by the analytical variance. To account for this, a nonparametric bootstrapping procedure was implemented in which individual transects were randomly resampled with replacement. In each step of the bootstrap iteration, the same number of transects for each replicate as in the original data was drawn. Survey effort and number of groups within the sampled spatial cells were totaled and merged with the information on average depth, temperature, and DFS for each sampled cell. The GAM model was again fit to these data and predicted values were generated. The bootstrap sampling was repeated 100 times, and the average and standard error of the bootstrapped predicted values were compared against analytical model fits.

Due to the complexity of the model selection process in the GAM analysis, including evaluating the most appropriate smoothing or linear functions, it was not possible to automate this process inside the bootstrap iteration loop. Model selection error is therefore not directly incorporated in the bootstrap estimation of variance; however, model fits are such that this source of error is likely to be small.

Separate GAM analyses were conducted for each management unit sampled during summer and winter. Plots of analytical and bootstrap predicted SPUE values as a function of habitat variables were compared across management units to infer regional patterns in the spatial distribution of bottlenose dolphins.

Results

Summer 2002 Survey

In the northern migratory unit, dolphin groups occurred almost exclusively in the shallow water depth stratum fairly close to shore (Figure 3). The analysis of deviance for the GAM model indicated that both depth and distance from shore were significant explanatory variables. However, distance from shore explained a larger amount of the total deviance. Depth provided no additional explanatory power once distance from shore was included in the model (Table 1). Both the analytical and bootstrap models indicated an steep decline in SPUE with increasing distance from shore. Variance estimates were similar for both approaches suggesting relatively little overdispersion in this data (Figure 9). There was no significant relationship between log

transformed group size and distance from shore (linear regression: F = 2.75, error d.f. = 69, model d.f. = 1, p = 0.103); however, group sizes tended to be smaller at increasing distance from shore (Figure 10).

The distribution of bottlenose dolphin groups in the northern North Carolina management unit was similar to that for the northern migratory unit. Distance from shore was a highly significant explanatory variable. Depth was also significant, but depth provided no additional explanatory power once distance from shore was included in the model (Table 2). The model indicates an exponential decline in SPUE with increasing distance from shore, and estimates of variance were similar for both approaches (Figure 11). There was no indication of a relationship between group size and distance from shore for this management unit (linear regression: F = 0.0003, error d.f. = 18, model d.f. = 1, p = 0.986, Figure 10).

In the southern North Carolina unit, there were no significant relationships between SPUE and the explanatory variables (Table 3), and dolphin groups were broadly distributed over the survey area (Figure 12). There was no significant relationship between distance from shore and log transformed group size (linear regression, F = 0.8719, error d.f. = 20, model d.f. = 1, p = 0.362); however, the two largest groups observed occurred within 3.5 km from shore (Figure 13a).

Bottlenose dolphin groups were also broadly distributed in the South Carolina management unit. There was a significant, though weak, relationship between SPUE and distance from shore and no other factor improved the model fit (Table 4). The model indicated relatively high SPUE values close to shore, a decline in sighting rates at intermediate distances, and another increase further away from shore (Figure 14). Distribution was generally more patchy further away from shore, with many spatial cells with no sightings and some cells showing a relatively high sighting rate. The variance estimates were similar between the bootstrap and analytical models; however, the bootstrap estimates were slightly higher. There was no significant relationship between group size and distance from shore in this unit (linear regression: F = 3.802, error d.f. = 28, model d.f. = 1, p = 0.061); however, the p-value was nearly significant. The regression line is shown in Figure 13b and indicates a decreasing group size

with increasing distance from shore. These data indicate that animal density is higher close to shore than further offshore; however, group density is more uniform across the sampled area.

In the Georgia management unit, the distribution of dolphin groups and the resulting GAM model were similar to the South Carolina unit. Both distance from shore and depth were significant explanatory factors. Distance from shore explained a larger amount of the deviance, and depth provided no additional information once distance from shore was included in the model (Table 5). As in South Carolina, there were higher SPUE values nearshore, a region of lower predicted SPUE values, and another higher density area further offshore. In this case, the variance estimated by the bootstrap model was lower than that for the analytical model. This is likely the result of the relatively small sample size in this management unit (Figure 15). There was no indication of a relationship between group size and distance from shore in Georgia (Figure 13c, linear regression: $F = 0.459$, error d.f. $= 26$, model d.f. $= 1$, $p = 0.503$).

Survey effort was only completed within the 0-20m depth stratum in the northern and central Florida management units (Figure 3), and therefore inferences about spatial distribution are restricted to areas relatively close to shore. In the northern Florida unit, depth, distance from shore, and temperature were all statistically significant in single factor models. However, distance from shore explained the highest amount of deviance in the data, and the other factors did not significantly increase explanatory power once distance from shore was included in the model (Table 6). In this case, the smooth function produced unrealistic predictions and error structure. A linear model explained the same amount of deviance and produced a more appropriate model fit (Table 6). The resulting model predicts a decline in SPUE with increasing distance from shore across the sampled area (Figure 16). There was evidence of decreasing group size with distance from shore; however, the linear regression was not significant due to low sample size and high variability (Figure 17a, linear regression: $F = 8.343$, error d.f. $= 2$, model d.f. $= 1$, $p = 0.1019$).

In the central Florida management unit, depth was the only significant explanatory factor, though other variables were nearly significant (Table 7). Both temperature and distance from shore provided no additional explanatory power once depth was included in the model. As in the

northern Florida unit, the smooth function resulted in unreasonable predicted values and error structure. The linear model for depth explained the same amount of deviance as the smooth function with more appropriate error structure. The model predicts a decline in SPUE over the sampled depth range (Figure 18). There was no evidence of a relationship between group size and depth for this management unit (Figure 17b, linear regression: F = 0.934, error d.f. = 9, model d.f. = 1, p = 0.3590).

Winter 2002 Survey

There were no bottlenose dolphin sightings north of Cape Henry on the southern edge of the mouth of Chesapeake Bay during the winter survey. Analyses for the North Carolina management unit therefore included transect lines from Cape Henry south. The GAM analysis indicated highly significant effects of depth, distance from shore, and temperature (Table 8). No groups were observed at temperatures < 9.5 ºC, and the SPUE values were variable with no trend at higher temperatures (Figure 19). The two northernmost sightings occurred in offshore waters warmer than 9.5 ºC (Figure 20). Temperature was recoded to a binary variable, and the distance from shore smooth function was nested within each level of the temperature code (Table 8). This nested model was highly significant and resulted in a good fit to the data. Predicted values for temperatures <9.5 ºC were equal to zero at all distance from shore values. Predicted values for the analytical and bootstrap models for temperatures >9.5 ºC indicated an exponential decline in SPUE with increasing distance from shore. Observed SPUE values indicated a slight increase in sighting rate at distances > 40 km from shore (Figure 21). There was a significant relationship between log-transformed group size and distance from shore in the North Carolina management unit (Figure 22, linear regression: F = 16.637, error d.f. = 115, model d.f. = 1, p = 0.0008). Animal density in this management unit is therefore highest in coastal waters and declines steeply with increasing distance from shore.

In the South Carolina management unit, all three explanatory variables were highly significant in single term models; however, depth explained the largest amount of deviance in the data (Table 9). Distance from shore did not provide any additional explanatory power once depth was included in the model. Temperature was also non-significant but only marginally so. The two term model including depth and temperature resulted in unreliable predicted values,

therefore the single-term depth model was retained. The resulting model indicated steeply declining SPUE values with increasing depth and a slight increase in SPUE at depths greater than 25 m (Figure 23). There was no indication of a relationship between group size and depth in these data (Figure 22, linear regression: $F = 0.374$, error d.f. $= 59$, model d.f. $= 1$, $p = 0.5433$).

Survey effort was only completed in the shallow water stratum in the Georgia management unit, therefore inferences about spatial distribution are limited to coastal areas. Distance from shore was the only significant explanatory variable, and it was only marginally significant (Table 10). The resulting GAM model was highly variable, but it indicated a decline in SPUE in coastal areas with a slight increase at distances greater than 30 km from shore (Figure 24). There was no significant relationship between group size and distance from shore in the Georgia management unit, though the largest group sizes (10-15 animals) occurred relatively close to shore (Figure 22, Linear regression: $F = 0.3476$, error d.f. $= 13$, model d.f. $= 1$, $p = 0.5656$).

Discussion

The GAM models indicate regional similarities in spatial distribution of bottlenose dolphins. In summer months, bottlenose dolphins in the northern migratory and northern North Carolina management unit were generally close to shore and showed a steep decline in occurrence with increasing distance away from shore. For both of these management units, sighting rates fell to zero at distances greater than 30 km from shore and were very low (< 0.01 groups / km effort) at distances greater than 20 km from shore. This is consistent with the general patterns apparent in the distribution of sightings from the survey, only 9 of 82 bottlenose dolphin groups sighted during the survey occurred in the 20-40 m depth strata (Figure 3). For both management units, there was a weak trend toward increasing group size with increasing distance from shore, but group sizes were highly variable. The vast majority of the bottlenose dolphin population lies within 20 km from shore in these regions, and animal densities are highest within 5 km from shore.

These results are consistent with previous analyses of spatial distribution of bottlenose dolphins from earlier surveys. In both the 1982 CETAP surveys (CETAP, 1982; Kenney, 1990) and the 1995 SEFSC surveys (Garrison and Yeung, 2001; Garrison, 2001) north of Cape Hatteras, NC during summer, bottlenose dolphins were observed to be most abundant close to shore with sighting rates dropping near zero further away from shore. However, in previous surveys it appears that spatial patterns were somewhat different from those during the 2002 surveys. For example, in the summer 1995 surveys sighting rates dropped to levels near zero at distances from 9-13 km from shore, and these distances were variable among repeated replicate surveys of the same area (Garrison, 2001). In an aerial survey of the area north of Chesapeake Bay during summer 1998, bottlenose dolphin groups were sighted further away from shore and did not show a similar decrease in density to that observed in the current survey (D. Palka, Northeast Fisheries Science Center, unpublished data). It appears that the spatial distribution of bottlenose dolphins in this region is variable both within and between years, suggesting a response to temperature variation. Additional analyses and comparisons between surveys across multiple years are being conducted to further evaluate these relationships.

The spatial patterns observed in this and previous studies suggest that the coastal morphotype is primarily distributed close to shore in the northern migratory and northern North Carolina management units, and that there is little mixing between the coastal and offshore morphotypes in these areas. The broad region, generally between 20-50 m depth, with very low sighting rates has been observed in multiple aerial surveys across a long period of time. In vessel surveys of deeper waters during 1998 (Mullin, in press) and 1999 (SEFSC, unpublished data) and on the offshore ends of the CETAP survey transects (Kenney, 1990) bottlenose dolphins were observed to occur in waters > 50 m depth and near the shelf break. The separation between these two populations is consistent with the hypothesis of little mixing of morphotypes in this region during summer months.

In management units further south, bottlenose dolphins were more broadly distributed across the sampled area during summer. In the southern North Carolina, South Carolina, and Georgia management units the sighting rates suggest higher group densities relatively close to shore, an area of relatively low density, and an area of somewhat higher density further offshore.

There is a weak indication of higher group sizes close to shore suggesting that animal density is higher in coastal areas; however, the high variability in group size reduces the importance of this relationship. It is more difficult to infer spatial patterns in the Florida management units due to the truncated sampling range.

Aerial surveys have not previously been conducted during summer months in these areas; however, the observed spatial patterns are generally consistent with those observed during a vessel survey of the continental shelf during summer 1999 (SEFSC, unpublished data). Bottlenose dolphin groups were encountered in relatively low densities across the continental shelf in depths greater than 10m out to the continental shelf break. The spatial patterns in these management units are also consistent with patterns observed during winter aerial surveys. There are no apparent breaks in spatial distribution in these regions that could be used to infer a separation between the coastal and offshore morphotypes. In both biopsy data and from visual identification of animals during vessel surveys, it is apparent that the spatial distribution of the two morphotypes overlaps in these areas during summer months.

During winter months, northern migratory animals move south and at least some mix with animals in the northern North Carolina and southern North Carolina regions (NMFS, 2001). The northern limit of this mixed North Carolina management unit is likely related to temperature either in response to movements of prey or metabolic limitations. In the current analysis, no bottlenose dolphins were observed in waters of temperatures < 9.5 ºC, which included all inshore waters north of Chesapeake Bay. Very few animals occurred in waters < 10.5 ºC, and the bulk of the groups in this management unit were observed in the region between Cape Hatteras and Cape Lookout at temperatures > 13 ºC due to the influence of the Gulf Stream (Figure 20). Group densities were also highest in this area during the winter 1995 aerial surveys (Garrison and Yeung, 2001). It is likely that variation in temperature patterns will result in interannual variability in both the northern limit and onshore-offshore distribution of bottlenose dolphins. During the current survey, both group densities (SPUE) and group sizes were highest in coastal waters indicating that the bulk of the bottlenose dolphin population occurred very close to shore in the winter North Carolina management unit.

In both the South Carolina and Georgia management units during winter, group sighting rates were highest relatively close to shore, followed by an area with low sighting rates and another area with increased sighting rates further offshore. However, the sampling range in the Georgia management unit was truncated. The 15-20 m depth interval identified as a low density area in the South Carolina unit corresponds to approximately 25-30 km from shore in this region and is consistent with the apparent increase in sighting rates in the Georgia unit at these distances. The general spatial patterns are also consistent with those identified during the 1995 winter surveys south of Cape Hatteras. An analysis of spatial pattern during winter 1995 suggested an area of low sighting rates at 27 km from shore with a region of somewhat higher sighting rates as distances > 50 km from shore (Garrison, 2001). These distances from shore correspond to the 25-30 m depth range in the South Carolina region.

In a previous analysis (Garrison, 2001), the apparent gap in distribution was used to infer a potential separation between the coastal and offshore morphotypes during winter months. However, it was noted that limited biopsy data available during winter months and the limited survey effort made these identified boundaries tentative. More recent biopsy sampling data has indicated that offshore morphotype animals occur inside the previously identified coastal morphotype habitat during winter, and coastal morphotype animals occur outside of this area (P. Rosel, unpublished data). Thus, no separation between the two populations should be inferred from these data.

The goal of this analysis was to describe the spatial distribution of bottlenose dolphins based upon the number of groups sighted per unit of survey effort in relationship to habitat variables. An implicit assumption in this analysis is that sighting probabilities are independent of the covariates included in the various GAM models. If, for example, sighting probabilities were significantly higher close to shore than further away from shore then the inferred spatial patterns would be confounded by this dependence. Because the same aircraft and observers were used throughout a survey, tracklines were laid perpendicular to depth and distance from shore gradients, and complete tracklines were conducted under generally the same environmental conditions (e.g., weather, glare, sea state), these factors are unlikely to introduce significant dependence between sighting probability and habitat gradients. However, one potential source

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of bias is the apparent trends in group size as a function of distance from shore and/or depth. Larger groups are more likely to be seen by observers because at least one animal of a large group is more likely to be on the surface. Thus, it is possible that larger average group size in water close to shore introduces dependence between covariates and sighting probabilities. The potential confounding between variable group sizes, environmental conditions, and sighting probabilities across spatial gradients limits the utility of the methods used here for generating an actual spatial model of bottlenose dolphin abundance across habitat variables. In the approach of Hedley *et al.* (1999), sighting probabilities were assumed to be equal across habitat gradients and for various group sizes. In cases where group sizes vary widely, as with the current study, spatial variation in sighting probability increases the complexity of these models and calculation of appropriate measures of uncertainty, and this is an ongoing area of research.

The analysis of spatial pattern identifies regional similarities in bottlenose dolphin distribution among management units. During summer months, areas north of Cape Lookout, NC (i.e., northern migratory and northern North Carolina units) are characterized by high group densities close to shore declining rapidly at distances > 20 km. South of this area, dolphin groups are distributed more broadly across the continental shelf. During winter months, the northern limit of bottlenose dolphin groups appears to be related to temperature with no animals occurring at temperatures < 9.5 ºC. Dolphin groups in the North Carolina management units occurred primarily close to shore, and in units further south groups were more broadly distributed consistent with patterns observed in previous winter surveys.

V. Distribution of Coastal and Offshore Morphotypes

Objective

      In previous assessments, a primary source of uncertainty was distinguishing between the coastal and offshore morphotype of bottlenose dolphins during aerial surveys. While abundance estimates for bottlenose dolphins in coastal waters can be developed, it is difficult to allocate between the two morphotypes in the absence of supplemental information. A previous analysis of available biopsy samples indicated overlapping distributions of the coastal and offshore morphotypes in waters between 6-81 km from shore during summer (Torres *et al.*, in press). The samples used in that analysis were primarily from the region south of Cape Hatteras, and there were very few samples available at that time in the region of overlap between the two morphotypes during summer, and there were no biopsy samples available from winter months. Spatial analyses were therefore used to define interim habitat definitions (Garrison, 2001). However, apparent gaps in spatial distribution do not necessarily indicate separation between the two morphotypes, and there was no estimate of uncertainty around these initial habitat definitions. Extensive systematic biopsy collection surveys were conducted in 2001 and 2002 concentrating on coastal and intermediate depth waters. The majority of these sampling efforts occurred during summer months; however, limited sample collection surveys were conducted during winter months of 2002.

      The goal of the current analysis is to evaluate the degree of spatial overlap between the coastal and offshore morphotypes. The analysis is conducted on a regional basis reflecting similarities in spatial patterns between management units described in section IV. We used logistic regression to evaluate the probability that a particular bottlenose dolphin group is of the coastal morphotype as a function of habitat variables. The resulting models are used to partition abundance estimates between the coastal and offshore morphotypes.

Methods
Definition of Regions

Since abundance estimates of the coastal morphotype are needed for each management unit separate models of morphotype distribution would ideally be developed for each unit. However, available sample sizes during both summer and winter do not allow separate models. Therefore, similarities in spatial patterns in bottlenose dolphin distribution among management units were used to define larger scale regions for the current analysis.

During summer, there were apparent differences in spatial patterns between management units north of Cape Lookout, NC (i.e., northern migratory and northern North Carolina) and those south of Cape Lookout (i.e., southern North Carolina, South Carolina, Georgia, and Florida units). In the northern region, dolphins occurred in coastal waters, and there was a steep decline in sighting rates with increasing distance from shore (Figure 3, Figure 9, Figure 11). In the southern region, dolphins were more broadly distributed. The highest sighting rates occurred close to shore, but dolphin groups also occurred further from shore (Figure 3, Figure 12, Figure 14, Figure 15). These general patterns and the differences in spatial distribution between northern and southern regions are consistent with previous findings during summer months (e.g., CETAP, 1982; Garrison, 2001). Given the strong regional differences in spatial distribution, it would be inappropriate to fit a single model to describe morphotype distribution coastwide.

Regional differences in sample distribution also necessitate division of the current analysis into northern and southern regions. In the northern region during summer, all biopsy samples were collected either close to shore or in deep waters near the shelf break with no samples in between (Figure 25). The bulk of the coastal morphotype samples were collected relatively close to shore in the northern migratory management unit (Table 11). This sample distribution reflects the underlying distribution of dolphins in the region. There has been extensive sampling effort in intermediate waters including intensive surveys by airplane during summer 2002, but no bottlenose dolphin groups were sighted or biopsied in this area. The logistic regression analysis cannot be used in cases where there is complete separation between samples (McCullagh and Nelder, 1989), and no inferences can be made about overlap between morphotypes at intermediate depths in the absence of samples. Thus, information from the spatial analysis was used to infer separation between morphotypes in the northern region, and logistic regression analysis was conducted only for samples from the southern region.

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In winter months, the regional differences in spatial patterns are not as clearly defined as those during summer. However, the North Carolina units did show rapidly declining sighting rates with increasing distance from shore (Figure 2, Figure 21), while in management units further south dolphin groups were more broadly distributed (Figure 2, Figure 23, Figure 24). Further, during winter months the number of available samples coastwide is small, and biopsy samples were collected almost exclusively in the Georgia and North Carolina management units (Figure 26, Table 12). The near complete lack of samples in the South Carolina region along with regional differences in spatial distribution precludes extrapolating across the entire shelf. Regression analyses were therefore conducted separately for samples collected in the North Carolina and Georgia management units.

Logistic Regression

The response variable being considered here is the binary response of a given sample being from an animal of the coastal vs. offshore morphotype. Previous analyses suggest that there is likely a gradient in the distribution of the two morphotypes. Habitats very close to shore likely contain exclusively coastal morphotype animals and areas further from shore contain exclusively offshore animals (Torres *et al.*, in press). This type of data structure is appropriately analyzed using logistic regression, a form of generalized linear model (GLM) using a logit link function and a binomial error structure to evaluate the relationship between continuous or nominal explanatory variables and a binary response (Agresti, 1990; McCullagh and Nelder, 1989). The logit function is given as:

$$(2) \quad p(z) = \frac{\exp\left(\theta_{int} + \sum_{r=1}^{R} \theta_r z_r\right)}{1 + \exp\left(\theta_{int} + \sum_{r=1}^{R} \theta_r z_r\right)} = logit^{-1}\left(\theta_{int} + \sum_{r=1}^{R} \theta_r z_r\right),$$

where *p(z)* is the probability of an event occurring (i.e. the probability of a coastal morphotype), θ_{int} is an intercept term, and θ_γ and z_γ are regression parameters and values for each of R covariates included in the model. Model selection and fit were evaluated using an equivalent analysis of deviance approach to that described in the spatial GAM analysis above (McCullagh

and Nelder, 1989). In addition to single-term models, two-term models were evaluated and interaction terms were investigated where possible given limited sample sizes.

Explanatory variables included depth, temperature, and distance from shore. The data values at each biopsy sample location were developed using the sources described above for the spatial analysis. The sampling unit for this analysis is a group of dolphins sampled at a particular spatial location as opposed to individual animals. The sample sizes given in Table 11 and Table 12 reflect sampling locations rather than the total number of individual animals sampled. There were several cases where "mixed" groups of animals occurred. Multiple biopsy samples were collected from a single group and included both coastal and offshore morphotype samples. These invariably occurred in relatively deep (> 20m depth) waters in the southern portion of the sampling range. For the purposes of the current analysis, these groups were coded as two samples, one coastal and one offshore, occurring at the same spatial location and environmental conditions. It is often difficult to collect more than one sample from a given dolphin group, particularly in offshore waters. Thus, the extent of this phenomenon cannot be evaluated using the current data.

Results

Summer Samples

In the northern region including the northern migratory and northern North Carolina management units, 25 coastal morphotype and 17 offshore morphotype groups were sampled. The furthest offshore coastal morphotype sample was collected at 18.3 m depth and 12.6 km from shore. The shallowest offshore morphotype sample occurred at 47.4 m depth at 43.3 km from shore. The closest to shore an offshore morphotype sample was collected was 36.9 km from shore at a depth of 240.6 m (Figure 27). There was no overlap between coastal and offshore morphotype samples, precluding any logistic regression analysis.

In the southern region, offshore morphotype samples were frequently collected from bottlenose dolphin groups occurring quite close to shore and in shallow water throughout the latitudinal range (Figure 25). Offshore morphotype samples often occurred in water depths < 20m. The shallowest offshore morphotype sample was collected at 12.8 m depth and 15.4 km

from shore. Coastal morphotype animals were less frequently sampled in locations further offshore. The furthest offshore coastal morphotype samples were collected at 30.9 m depth and 74.6 km from shore in southern North Carolina and at 34.6 m depth and 82.5 km from shore in northern Florida. In both cases, at least one offshore morphotype animal was also sampled from the same group of animals.

The analysis of deviance indicated that both depth and distance from shore had highly significant explanatory power, and temperature was also significant (Table 13). Of these, depth had the greatest explanatory power, and no other term added significant information once depth was included in the model. There were no significant two-term interaction effects. The logistic regression model predicted a decreasing probability of a bottlenose dolphin group being of the coastal morphotype with increasing depth (Figure 28). The 95% confidence limits of the model predictions are large due to relatively low sample size and the high degree of overlap between the two morphotypes in this region during summer.

Winter Samples

The sample size in the North Carolina management units during winter months was quite small and included 21 coastal morphotype samples and only 5 offshore morphotype samples. One offshore sample was collected in relatively shallow water at 16.8 m depth and 7.3 km from shore. The furthest offshore coastal morphotype sample was collected at 17.2 m depth at 11.7 km from shore.

Both distance from shore and temperature explained significant portions of the deviance in the data; however, no model fit was possible for depth due to nearly complete separation of samples. Temperature was the more important factor and distance from shore provided no additional explanatory power once temperature was included in the model (Table 15). While the analysis of deviance indicated that temperature provided significant explanatory power relative to the null model, the maximum likelihood estimates indicated that it was only nearly significant as a model predictor (Table 16). The model indicated a decline in the probability of a coastal morphotype group with increasing temperature; however, the 95% confidence limits of the odds ratio include 1 indicating that the strength of this effect is questionable. The uncertainty in the

model fit is reflected in the very large 95% confidence limits of predicted values ([Figure 29](#)). The model suggests that dolphin groups occurring in waters > 20ºC are more likely to be of the offshore morphotype. This corresponds to warm water further away from shore associated with the Gulf Stream.

Sample sizes were also small in the southern region during winter with 13 coastal morphotype samples and 4 offshore morphotype samples. Only one offshore sample from South Carolina was included in the analysis, therefore these analyses should be considered more representative of the Georgia management unit. One coastal morphotype sample was collected well offshore at 112 km from shore at 38.4 m depth. Offshore morphotype samples were collected at the same location. The offshore morphotype sample collected closest to shore was at 40.3 km from shore in 21.9 m depth.

Depth, distance from shore, and temperature all explained significant amounts of deviance, and depth was the most important factor. Temperature provided no additional explanatory power once depth was included in the model ([Table 17](#)). It was not possible to evaluate the two term model including depth and distance from shore as this model resulted in complete separation of the data invalidating the logistic regression. The maximum likelihood estimates indicated that depth was a significant predictor, and the probability of a coastal morphotype sample declined with increasing depth ([Table 18](#)). However, the model fit and 95% confidence intervals of predicted values remain very uncertain given the small sample size ([Figure 30](#)). The uncertainty is particularly high in waters > 40m depth due to the very limited number of offshore samples collected.

Discussion

The results of the current analysis are consistent with those of previous studies and the general understanding of the relative distribution of the two morphotypes in Atlantic coastal waters. During summer months north of Cape Lookout, it appears that there is little or no mixing between the two populations, and that the coastal morphotype aggregation can be defined based upon spatial patterns. No samples from offshore morphotypes have been collected to date in waters < 40 m depth or within 40 km from shore in this region. However, this does not

preclude the possibility of mixing between the two morphotypes. For example, the bathymetry gradient is notably compressed around and just south of Cape Hatteras, and deep water occurs close to shore in this area. It is certainly possible that offshore morphotype animals could occur relatively close to shore or that coastal morphotype animals could stray into deep waters. Similarly, in the majority of surveys flown to date, there has been clear separation between a nearshore and offshore aggregation of bottlenose dolphins. However, during a summer 1998 survey, there was no clear spatial separation in areas north of Chesapeake Bay (D. Palka, Northeast Fisheries Science Center, unpublished data). Interannual variability in morphotype distribution cannot be directly evaluated given the difficulties in collecting samples over large spatial scales. For the northern region during the summer, spatial patterns from each newly conducted survey should be analyzed to evaluate both the degree of separation between the two morphotypes and the habitat range for the coastal morphotype in a given year.

South of Cape Lookout during summer months, the degree of mixing between the two morphotypes is very high, and offshore groups occurred very close to shore in this region. The bathymetry gradient is shallow in this region with depths <40 m occurring up to 100 km from shore, and water temperatures are generally uniform across the shelf during summer months until reaching the very warm Gulf Stream water off the shelf break. Given the general homogeneity in habitat characteristics, it is not surprising that there is no clear distinction between offshore and coastal morphotype habitats in this region.

Despite extensive sampling efforts over the last several years, the number of samples collected south of Cape Lookout in summer remains relatively small, and there are a number of significant spatial gaps. Most notably, there are very few samples in both coastal and offshore waters of South Carolina, in areas close to shore in North Carolina, and in intermediate depths (20-50 m) in southern North Carolina (Figure 25). These gaps in sampling distribution, the generally low sample size, and the high degree of mixing between morphotypes result in the large amount of uncertainty around the logistic regression curve. Additional sampling effort targeting these gaps would reduce the uncertainty and make conclusions regarding morphotype distribution more robust.

The sampling problems are more severe in winter and make any conclusions about morphotype distribution tentative at this time. The sampling efforts in North Carolina were primarily limited to local areas just south of Cape Fear and Cape Lookout. The goal of these efforts were primarily to improve definition of latitudinal stocks, and therefore they did not attempt to include broader coverage further offshore. Some limited sampling effort was attempted in the region between Cape Lookout and Cape Hatteras; however, very few samples were collected in this area where the majority of bottlenose dolphin sightings occurred during the aerial survey (Figure 26). In addition, samples were collected in this region between late October and late March. While this time period corresponds to the winter season defined in the previous assessments (NMFS, 2001), there are potentially significant changes in the temperature regime across this time period, and the distribution of animals may not be representative of the January – February time frame of the aerial survey. The application of the logistic regression analysis implicitly assumes that the spatial distribution observed in these samples is representative of the spatial distribution of bottlenose dolphins during the aerial surveys. Given the sources of potential sampling bias this assumption is not necessarily accurate.

Similar sampling biases affect the analysis of samples from the Georgia management unit. Coastal sample collections were conducted by small vessels that did not range into offshore waters between early February and mid-March. Samples from offshore waters were collected during a large-vessel survey in late March. There are no samples from intermediate waters between 10–40 km from shore, since little survey effort has been expended in this region. The total number of samples for this analysis is small, and there were very few offshore samples. As a result, there is a high degree of uncertainty, and the collected samples may not be representative of the spatial distribution of bottlenose dolphins in this region.

The limited sample sizes during both winter and summer reflect the logistic difficulties and expense of collecting biopsy samples. These problems are particularly severe during winter months when weather conditions are rarely favorable for sample collection with small vessels that are able to pursue dolphins. The most appropriate sampling platforms also have limited range, and they do not have a capability to sample far from shore where the degree of mixing between the two morphotypes is expected to be highest. Despite this, biopsy sampling and

genetic identification are the only available methods for positive distinction between the two morphotypes. Several additional options are currently being explored. These include using photo-identification and visual characteristics of animals to identify coastal vs. offshore morphotype animals during vessel surveys. In addition, using aerial photography during aircraft surveys to identify animals based upon morphometric differences is currently being explored. These methods may provide a more efficient and complete picture of morphotype distribution during a particular survey but would still ultimately need to be confirmed by biopsy sampling and genetic identification.

Despite these uncertainties, the current approach improves the assessment of morphotype distribution in coastal Atlantic coastal waters. The inferred gradients in distribution more appropriately reflect the biological reality than the spatial boundaries described in previous analyses. In addition, this approach directly quantifies the uncertainty due both to limited sample size and the biological complexity. The potential biological removal (PBR) benchmark explicitly accounts for statistical uncertainty in the abundance estimate. The relative distribution of coastal vs. offshore morphotypes remains the most significant source of uncertainty. The current approach allows direct incorporation of this uncertainty into abundance estimate and the resulting PBR levels for bottlenose dolphin management units.

VI. Abundance of Bottlenose Dolphins

<u>Objective</u>

In this analysis, we estimate the abundance of bottlenose dolphins in coastal waters of the U.S. between 0-40m depth. Previous abundance estimates based on surveys conducted in 1995 included several sources of bias and uncertainty. First, the earlier surveys were not based on the current management unit definitions and therefore did not include complete coverage of some management units. Second, there was a notable decline in the probability of seeing animals near the trackline, and this was dealt with analytically by left truncating the data rather than fitting a unimodal sighting function. Finally, the abundance estimates were not corrected for potential visibility bias (Garrison & Yeung, 2001). The current analysis addresses these sources of bias and updates the abundance estimates for bottlenose dolphins. These estimates include both coastal and offshore morphotype bottlenose dolphins within the surveyed area.

<u>Methods</u>

Distance analysis of line transect sampling

The standard theory for line-transect sampling is well developed and is routinely applied in wildlife population assessments in both terrestrial and marine habitats (Buckland *et al.* 1993). Given a random distribution of a survey transect relative to the distribution of a population of interest, the probability of an animal occurring at any distance away from the transect line is equal. If all groups of animals within a particular distance (W = half strip width) on either side of the line are observed, the group density in the area is:

$$(1) \quad D = \frac{n}{2LW},$$

where *n* is the number of groups observed and *L* is the length of the transect line.

However, line transect theory (Buckland *et al.*, 1993) recognizes that the probability of observing an animal or group generally declines with increasing distance from the trackline (i.e., perpendicular sighting distance, PSD). The distance sampling approach therefore examines the distribution of sighting frequency as a function of PSD and corrects the density estimate for the sighting function, g(x). The sighting function can take any integrable form, however in practice

it is generally constrained to be monotonically decreasing vs. PSD (x). To calculate the probability of sighting an animal within the surveyed strip, the sighting function is rescaled to the probability distribution function (pdf), $f(x)$ as:

$$(2) \qquad f(x) = \frac{g(x)}{\int_0^w g(x)dx} .$$

The assumption is made that the sighting probability on the trackline is unity ($g(0) = 1$) allowing one to solve for the pdf at x = 0 as:

$$(3) \qquad f(0) = \frac{1}{\int\limits_0^w g(x)dx} .$$

The probability of sighting an animal within a strip is then the area under the sighting function divided by the total half strip width:

$$(4) \quad P_a = \frac{\int_0^w g(x)dx}{W} .$$

and the quantity µ, or the effective strip width is:

$$(5) \qquad \mu = P_a \cdot W = \int\limits_0^w g(x)dx ,$$

The density estimate given in equation 1 is therefore modified to:

$$(6) \quad D = \frac{n}{2L\mu} .$$

In cases where animals occur in groups of individuals, such as dolphin groups, the appropriate unit of detection is the group. The density of groups given in equation 6 is multiplied by mean group size, $E(s)$, to solve for the density of individuals in the surveyed area.

$$(7) \qquad D = \frac{n \cdot E(s)}{2L\mu} .$$

A potential source of bias in the expected group size is a tendency for larger groups to be more readily observed at larger distances away from the trackline than smaller groups. Group size bias is accounted for by correcting the value of E(s) using a regression of log group size against PSD.

There was no evidence of group size bias in the current analysis, and the mean group size is used for $E(s)$ throughout.

Fitting a unimodal sighting function.

The standard distance analysis approach assumes that sighting probability is a monotonically decreasing function of PSD. Typical sighting functions include the half-normal and hazard rate functions, both of which may include a shoulder of constant sighting probability near the trackline. Adjustments to the curve shape is implemented by including cosine or hermite polynomial adjustment terms in the function (Buckland *et al.* 1993).

However, sighting rates are frequently not monotonically decreasing in aerial survey data. This has been noted in previous studies and generally results from a blind spot directly beneath the aircraft when looking out of a flat window. Bubble windows, such as those used in the current survey, allow the observers to see directly beneath the aircraft; however, the position is uncomfortable and there is a tendency for observers to focus attention at some distance away from the trackline. It is appropriate in these cases to fit a flexible unimodal sighting function and replace the assumption of 100% visibility on the trackline with the assumption that there is some perpendicular sighting distance, d_{max}, away from the trackline at which the sighting probability = 1. Several different approaches have been taken to fitting a flexible unimodal model. Quang and Lanctot (1991) used a "truncated beta function" fitting a unimodal curve using the incomplete beta function. Kingsley and Reeves (1998) used a sinusoidal function to fit the increasing portion of the sighting curve between 0 and d_{max} and the standard hazard function to fit the declining portion of the sighting curve.

We have taken a non-parametric approach to modeling the sighting function using smoothing splines to provide increased flexibility in fitting the curve. The function (implemented in S-Plus, MathSoft Inc.) is a cubic spline that minimizes the compromise between fitting the observed data and smoothness of the curve. The degrees of freedom of the smooth spline can be specified to adjust the degree to which the curve smooths variation in the data (Venables and Ripley, 1997). In our analysis, we examined the smooth spline fit to observed sighting frequencies specifying between 4-9 degrees of freedom. The shape of the curve within

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this range was consistent and resulted in a smooth unimodal function that did not overfit noise in the observed data.

Estimating perception bias

Using the unimodal sighting curve, the assumption of perfect sightability along the trackline is replaced by the assumption of perfect sightability at d_{max}. This approach is therefore still susceptible to visibility bias. Estimating visibility bias requires modification of standard line transect survey methods. In general, this involves the use of an additional team of observers stationed either on the same platform or a different platform from the primary observer team (Buckland *et al.* 1993). The majority of analytical methods for two-team visual line transect surveys employ a combination of line-transect and mark-recapture approaches (MRLT, Borchers *et al.* 1998, Laake 1999). These methods treat observations by the two teams as a sight-resight event. In an analogy to mark-recapture approaches, the initial sighting of a group of animals is considered a marking event, and a subsequent sighting of the same group is a recapture event.

The MRLT methods build on the basic theory underlying the classic Lincoln-Peterson estimator,

$$(8) \qquad n = \frac{n_2}{n_{both}/n_1},$$

where n is the estimated abundance, n_1 is the number of animals marked in the initial capture, n_2 is the total number of animals collected in the second capture, and n_{both} is the number of marked individuals recovered during the second capture. The mark-recapture estimator assumes that the population is closed (i.e., no immigration or emigration) between the mark and recapture events and the probability of capturing an animal is not affected by the marking event. For line-transect surveys, the first assumption is generally not problematic as the two sighting events occur close together in time. However, the second assumption is the primary issue that must be addressed in both survey design and the analytical framework.

The second assumption can be restated that the sighting and resighting events are assumed to be independent of each other. In the case of a two-team survey, the sighting of a

group by team 1 cannot influence the probability of resighting that group by team 2. Thus, during two-team surveys, it is important that the teams search independently of each other and do not cue each other to sightings. However, the relationship between sighting probability and distance away from the trackline (or other covariates) imparts dependence between the teams (Borchers 1996, Laake 1999). Both teams have a reduced probability of sighting animals that are further away from the trackline, and this causes covariance between the resighting rates. If the factor affects the observers in the same way (i.e., positive covariance) then the abundance in equation 8 will be an underestimate (Borchers 1996, Laake 1999). The independence assumption is therefore modified to a conditional independence assumption (CI) such that sightings between teams are independent conditional on covariates that influence sighting probability.

The distance sampling framework deals explicitly with distance away from the trackline as the primary covariate influencing sighting probabilities that induces dependence between sightings by the two teams. However, additional covariates can also affect the sighting probability. The line transect models developed by Borchers *et al.* (1998) in parallel with Alpizar-Jara and Pollock (1996), Manly *et al.*(1996) and Quang & Becker (1997) make the assumption that conditional independence is satisfied at all distances away from the trackline. Laake (1999) termed this the full conditional independence (FCI) assumption, and this method requires investigation of all possible covariates in formulating the sighting probability function to develop a reliable estimate. However, Laake (1999) investigated the effects of relaxing this assumption to assume only that sighting rates are conditionally independent on the trackline (Trackline Conditional Independence, TCI). The likelihood models for the TCI assumption on sight-resight rates of wooden stakes provided a more accurate estimate of abundance than those under the FCI assumption (Laake 1999).

Palka (1995) employed a somewhat simpler method that also applied the TCI assumption. Her estimator, termed the Direct Duplicate estimator (DD), used standard distance analysis methods to generate abundance estimates that account for the dependence of sighting rates on distance from the trackline. This estimator is a direct modification of the Lincoln-

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Peterson estimator in equation 8 to include calculated abundances rather than simply the number of sightings by each team:

$$(9) \qquad \hat{N}_c = \frac{\hat{N}_2}{\hat{N}_{both} / \hat{N}_1} ,$$

where N_1 is the abundance estimate using all sightings by team 1, N_2 is the abundance estimate using all sightings by team 2, and N_{both} is the abundance estimate based upon sightings by both teams. The DD estimator provided similar estimates for the abundance of wooden stakes compared to the likelihood models under the TCI assumption (Laake 1999). However, the DD estimator may be less reliable if the sight-resight rates and/or the total number of sightings are low. Variance is estimated by bootstrapping since the abundance estimates share common sightings (Palka 1995).

Since we are using a non-parametric approach to fit the sighting function, the likelihood models described in Laake (1999) could not be directly applied. Instead, we employed the DD estimator with a bootstrapping procedure to estimate variance in abundance estimates corrected for perception bias.

Bootstrap resampling and calculating densities

A nonparametric bootstrapping approach was used to develop density estimates and calculate variances for the terms in equations 7 and 9. The independent sampling unit for these surveys is the transect. The original survey design allocated effort by management unit and depth stratum (0-20 m and 20-40 m strata) using two replicate sets of transects (see Aerial Survey Design above). In each iteration of the bootstrap procedure, line transects were randomly resampled with replacement selecting the same number of replicate 1 and 2 transects as in the original design.

The bottlenose dolphin groups associated with the randomly selected transects were used to develop density estimates for each iteration. There were three classes of sightings during the

survey: those seen by team 1 only (n_{10}), those seen by team 2 only (n_{01}), and those seen by both teams (n_{11}). Distance estimation using the smooth unimodal sighting function was used to estimate parameters in equation 9. N_1 used all groups seen by team 1 ($n_{1.} = n_{10} + n_{11}$), N_2 used all groups seen by team 2 ($n_{.1} = n_{01} + n_{11}$), and N_{both} used only groups seen by both teams (n_{11}). Sightings were classified directly during the survey as every dolphin group seen by either team was circled for group size estimation and species identification.

For each class of sighting, a global smooth spline sighting function was fit across sightings from all management units and strata. Sightings were truncated at 630 m PSD during both summer and winter surveys, corresponding to the last defined angle interval. The smooth spline sighting function, $g(x)$, was fit to observed sighting frequencies in small 20 m distance interval bins. The resulting curve was rescaled to the probability distribution function, $f(x)$, by rescaling to 1 at the distance with the maximum predicted sighting frequency, d_{max}. The resulting curve was integrated numerically across the survey half-width to solve for $f(d_{max})$ and the effective strip width. The curve fit and predicted effective strip width was robust to a range of degrees of freedom of the spline smoother and different binning intervals for observed sighting frequencies. In test data where there was no drop off near the trackline, the smooth function gave very similar results to the standard parametric curves used in distance analysis.

The total number of groups, mean group size, and survey effort were calculated for each management unit and depth strata. Density estimates for each sighting type (D_1, D_2, and D_{both}) were calculated using equation 7. Finally, the direct duplicate estimator for corrected density, D_c was calculated (equation 9). Animal densities were multiplied by strata areas to obtain abundance estimates.

The bootstrap resampling loop was repeated 999 times, and the 1000th instance was the observed data. Means and standard deviations from the bootstrapped distributions are presented as estimates of animal abundance by stratum. The perception bias correction, $g(d_{max})$, was calculated for team 1 and 2 as N_1/N_c and N_2/N_c.

Results

Summer Survey

A total of 185 bottlenose dolphin groups were observed on effort during the summer surveys. 30 of these were seen only by team 1, 54 were seen only by team 2, and 102 were seen by both teams. The total number of groups, survey effort and strata areas are shown in Table 19. Survey effort and sighting locations by strata are in Figure 3.

The sighting function for both teams was strongly unimodal with maximum sighting rates approximately 148 m from the trackline (Figure 31). The estimated effective strip width for team 1 was 280.52 m (%CV = 6.26), 283.38 m (%CV = 5.79) for team 2, and 262.72 (%CV = 6.38) for sightings by both teams.

The individual density estimates for each team are given in Tables 20-22 and the corrected density and abundance estimates are in Table 23. The estimated $g(d_{max})$ values were generally > 0.5 for most management units and strata. In several cases, $g(d_{max})$ estimates were > 1 owing to small sample sizes in some strata (Table 23).

Winter Survey

During the winter 2002 survey, 185 groups of bottlenose dolphins were sighted. Of these, 21 were seen only by team 1, 39 by team 2 only and 125 were seen by both teams. Survey effort and sightings by strata are shown in Figure 2, and survey effort and numbers of dolphin groups by strata are in Table 24.

The sighting function for both teams was again unimodal with maximum sighting rates approximately 117 m from the trackline (Figure 32). The estimated effective strip width for team 1 was 273.13 m (%CV = 5.32), 275.82 m (%CV = 5.09) for team 2, and 260.42 (%CV = 5.10) for sightings by both teams.

The individual density estimates for each team are shown in Tables 25-27, and estimates corrected for perception bias are in Table 28. The $g(d_{max})$ estimates were generally higher than those during the summer survey and ranged between 0.58 – 1.

Discussion

The approach taken here addressed two sources of bias identified in previous bottlenose dolphin abundance estimates (Garrison and Yeung 2001). The flexible unimodal sighting

function is preferable to other options such as left truncation of the data, combining angle intervals to force the data to fit a monotonically declining curve, or ignoring the drop-off near the trackline. These options overestimate sighting probabilities near the trackline and therefore underestimate abundance. The nonparametric smoothing spline is a flexible curve that provides a robust estimate of sighting probability as a function of perpendicular sighting distance.

The two-team approach and the Direct Duplicate estimator accounts for the effects of perception bias. In general, these corrections were relatively small particularly for team 2 and during the winter survey. Less experienced observers were used during the summer survey than the winter survey. Previous studies have established that observer experience can have a significant effect on sighting probabilities (Laake *et al.*, 1997). The $g(d_{max})$ values were generally lower and d_{max} was generally higher for observers during summer months. Laake *et al.*(1997) estimated the perception component of $g(0)$ to be 0.865 for experienced observers. In an aerial survey for bottlenose dolphin in California, Forney *et al.* (1995) also estimated relatively high detection probabilities that were dependent on group size. The perception bias component of $g(0)$ for these surveys was 0.67 for group sizes 1-10 and 0.85 for groups >10. The results of the current study indicating relatively low perception bias is consistent with these previous studies.

The %CV values for the corrected abundance estimates were close to target CVs for the highest priority management units and strata. However, the abundance estimates were highly variable in areas where sighting rates were low such as the Florida management units during summer and in the offshore strata. Much of this variability was due to high variation in encounter rates or relatively low survey effort in lower priority areas. However, in the case of the southern and northern North Carolina units during summer, group sizes were also highly variable and contributed a significant amount of variability to the overall estimate.

While the effect of perception bias has been estimated in this analysis, the magnitude of availability bias has not been included, and this is a potential source of negative bias in the estimates. Since the observer teams are on the same platform, bottlenose dolphin groups are effectively available (i.e., at the surface) simultaneously to both teams. Therefore, it is not

possible to directly estimate availability bias with the current data. However, because group sizes were relatively large for most management units, we expect that this source of bias is relatively small. Large groups of dolphins are effectively available to the survey at all times because there is a high probability that at least one animal will be on the surface during the period the group is within visual range of the aircraft (D. Palka, NEFSC, unpub. analysis). This is particularly the case for delphniids that have relatively short dive-surface intervals. However, additional modeling studies incorporating animal and observer behaviors are required to better evaluate the extent of this bias for the current surveys.

The current analysis estimates the abundance of bottlenose dolphins in coastal waters between 0-40 m depth on the U.S. continental shelf. These estimates do not include animals occurring inside estuaries that may belong to the management units being considered here, and they do not distinguish between morphotypes. The logistic regression models and spatial analyses described above will be used along with the current analysis to estimate the abundance of the coastal morphotype and appropriate measures of uncertainty.

VII. Abundance of the Coastal Morphotype of Bottlenose Dolphin

<u>Objective</u>

Prior assessments of the coastal morphotype of bottlenose dolphin have been confounded by overlap with the offshore morphotype and inability to distinguish the two during visual surveys. The logistic regression models using genetic analysis of biopsy samples demonstrate considerable overlap between the offshore and coastal morphotypes, particularly in areas of North Carolina and further south. The abundance estimates developed in the previous section encompass habitats between 0-40 m depth, and these estimates likely include both offshore and coastal animals. To develop abundance estimates for the coastal morphotype, the current analysis combines the results of the logistic regression and spatial analyses with abundance estimates. Variability in both abundance estimates and the regression models are incorporated into the final abundance estimate to provide appropriate measures of uncertainty.

<u>Methods</u>

The logistic regression models predict the probability that a particular group of animals will be from the coastal morphotype as a function of environmental covariates. For those management units where valid logistic regression models could be developed, generating an abundance estimate for the coastal morphotype is most directly expressed as:

$$(1) \quad D_c = \int_0^X D(x \mid z) P(x \mid z) dx \, ,$$

where the integration is across a spatial domain X. D(x|z) is a spatially explicit density estimate conditional on a vector of environmental covariates z, and P(x|z) is the probability that animals at spatial location x are from the coastal morphotype, also conditional on environmental covariates.

However, deriving appropriate uncertainty estimates for a spatial model of animal density when encounter rates, sighting probabilities, and group sizes are all variable and potentially correlated is not straightforward. Likewise, it is difficult to derive an appropriate analytical solution that both solves for the variance of the integral of the logistic regression curve and accounts for covariance between the terms in the above integral. Therefore, we have again

resorted to a bootstrapping approach that simultaneously accounts for the sources of variability in the abundance estimates and prediction of the number of coastal animals within the survey region.

Recall that the density estimate based on line transect surveys is expressed as:

$$(2) \quad D = \frac{n \cdot E(s)}{2L\mu} .$$

In the absence of group size bias in sighting probabilities, the term in the numerator is equivalent to the number of individuals in the survey area or simply:

$$(3) \quad N_{individuals} = \sum_{i=1}^{n} s_i ,$$

where s_i is the number of animals in group i for each of n groups. Each group of animals is observed at a spatial location and is associated with environmental variables temperature, depth, and distance from shore determined either by observation or the data sources described in previous sections. The probability that group i is from the coastal morphotype can thus be predicted from the logistic regression equations, and the number of coastal animals within the area is then:

$$(4) \quad N_{coastal} = \sum_{i=1}^{n} s_i \cdot p_i(z) .$$

The number of coastal animals is the numerator in equation 2 and solves for the density of coastal morphotype animals within a stratum.

This approach makes two primary assumptions. First, that the spatial locations and associated environmental conditions where animals are observed during the survey are representative of the actual underlying spatial distribution and habitat of the population. Since transects are laid randomly with respect to the habitat and distribution of the animals, this assumption is likely met with good survey design. Second, we assume that group sighting probabilities are independent of the spatial location of the group and the environmental variables. This assumption is implicitly made when fitting a global sighting function across strata, and so is at least consistent with the assumptions of the distance analysis. In addition to these

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assumptions, we are again assuming that the logistic regression curve is derived from samples representative of the spatial distribution of the two morphotypes, an issue discussed in previous sections.

Estimating the variance in the density of coastal animals requires incorporating uncertainty in the logistic regression in addition to that in the density estimate. This combination was accomplished by embedding a parametric bootstrapping approach to simulate uncertainty in the logistic regression curves within the nonparametric loop that estimated variance of the density estimates. The logistic regression curve generates a normally distributed linear predicted value for each observation, i, as a function of the explanatory variables:

$$(5) \ \ln\left(\frac{p_i}{1-p_i}\right) = \alpha + \sum_z \beta_z x_i \ ,$$

and generates an estimate of standard error for the linear term. At each iteration loop, a random deviate from a normal distribution with a mean equal to the linear predictor and standard deviation equal to its standard error was generated for each observed bottlenose dolphin group. This random predicted value was then transformed to the predicted probability, p_i, that the group was from the coastal morphotype. The randomized probability was multiplied by group size as in equation 4, and the density estimation proceeded as normal.

The nonparametric bootstrap loop was identical to that described in Section VI and generates separate estimates for each team and the density estimator corrected for perception bias. The bootstrap was repeated 999 times, with the 1000th instance being the observed data and predicted probabilities from the regression curves. The resulting estimate and associated measures of uncertainty thus directly account for potential correlation between environmental covariates and group density, group size, and the probability of being from the coastal morphotype. The total abundance of coastal morphotype animals across the 0-40m depth sampling range for each management unit was calculated by summing corrected abundance estimates (N = D * Stratum Area) across strata for each bootstrap sample. The average and

standard deviation of the bootstrap estimates are the estimates for total coastal morphotype bottlenose dolphin abundance for each management unit.

For each management unit, the appropriate regional logistic regression model was used to generate predicted probability coastal values for each observed group. However, in the case of the northern migratory and northern North Carolina units during summer, no valid logistic regression model could be developed. In these cases, the spatial pattern in sighting frequency was used to infer a distance from shore boundary. Inside this area, all observed groups were assumed to be from the coastal morphotype and outside that area all were assumed to be from the offshore morphotype. In each case, the SPUE curve was examined to identify the location where the lower bound of the 95% confidence interval included zero sighting rates (Figure 9, Figure 11). This distance corresponded to approximately 25 km from shore for both management units. In each case, this resulted in only 1 sighting being classified as the offshore morphotype for each unit.

Results

For the summer survey, the individual team abundance estimates are presented in Table 29-Table 31, and the combined estimates corrected for perception bias are shown in Table 32. Predictably, the abundance estimates for the northern North Carolina and northern migratory management units differ very little from those not accounting for the relative distribution of coastal vs. offshore morphotypes since the vast majority of sightings in both management units occurred inside the 25 km boundary. However, estimates for the southern management units were on the order of 50-80% of the estimates for all dolphins in the 0-20 m strata and 10-20% of the standard estimates in the 20-40m strata (Table 32). The bulk of the sightings in these regions occurred between 6-30 m depth, and the predicted proportion of coastal groups ranged between 0.8 to 0.1 across this range (Figure 33). Despite the relatively high variability around the predicted logistic regression curve, the %CV values for the estimates for the coastal morphotype were only 5-10% higher than the standard estimates, with the exception of the southern North Carolina management unit. Combined abundance estimates and confidence limits across strata by management unit and combined %CVs are shown in Table 33.

Individual team estimates and combined estimates for the winter survey are given in Table 34-Table 37. In the North Carolina management units, the coastal morphotype estimate is approximately 10% lower than that of the standard estimate in the shallow stratum (Table 37). The majority of the sightings in the North Carolina management units occurred at temperatures between 11-16 ºC where the proportion of coastal animals is predicted to be very high based on the logistic regression (Figure 34a). The coastal morphotype estimates in the southern strata were approximately 10% below those for the standard estimates in the 0-20 m depth strata, but were substantially lower in the deep stratum in South Carolina. The bulk of the sightings in the southern management unit occurred between 0-18 m depth where the predicted proportion of coastal animals was high (Figure 34b). Despite the high variability in the logistic regression curve, the %CVs of the abundance estimates for the coastal morphotype were generally similar to those of the standard estimates. The combined abundance estimates across the depth strata for each management unit and associated confidence limits are shown in Table 38.

Discussion

The greatest source of unquantified uncertainty in these estimates is whether or not the logistic regression curves are representative of the spatial distribution, particularly during the winter months. As noted in the discussion of the logistic regression results, the numbers of samples used to generate these curves is small and they may not be representative of the entire sampling range due to the localized nature of the biopsy sampling. It is likely that these curves will be sensitive to the addition of new samples, and this may impact the abundance estimates for coastal morphotype animals during winter months. For example, in the North Carolina management unit, very few samples were collected from the region between Cape Lookout and Cape Hatteras, NC, where the bulk of the sightings occurred during the winter survey. The current logistic regression curve predicts that the bulk of the animals in this region are from the coastal morphotype associated with water temperatures between 11-16 ºC. The model predicts that offshore animals are restricted to even warmer waters further offshore, but this inference is based on only 4 offshore morphotype samples collected in deep water (Figure 26). Additional biopsy samples in this region are necessary to improve the robustness of the current model. A

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similar situation exists in southern regions during winter months since the sampling effort was limited to a small area in Georgia.

During summer months in the northern North Carolina and northern migratory units, a somewhat qualitative decision was made as to where to draw the boundary between the coastal and offshore morphotype animals. The only information available from available biopsy samples is that the boundary lies somewhere between 12.6 – 36.9 km from shore (Figure 27). The spatial pattern suggests separation between the two morphotypes and that 25 km from shore is an appropriate boundary. However, in the absence of additional biopsy sampling it is difficult to either precisely define a boundary or quantify the uncertainty in that decision. However, given the spatial distribution observed and the lack of offshore morphotype samples close to shore, it appears that the bulk of the sightings during the summer survey were of the coastal morphotype.

The relatively high uncertainty in the logistic regression curves did not significantly increase the uncertainty in the abundance estimates for the coastal morphotype. This is to some degree expected since we are essentially averaging across these models when combining them with the abundance data. However, the high uncertainty may introduce bias in some cases. In particular, the upper limit of these curves is constrained to 1. As a result, random samples of the linear predictor will tend to result in more probability values below the predicted curve than above it due to the asymmetry in the back-transformed confidence bounds (e.g., Figure 34a). This may appropriately reflect the uncertainty in the model; however improving the precision of the logistic regression models with additional samples will remove this potential source of bias.

VIII. Conclusions

The abundance estimates for the coastal morphotype of bottlenose dolphin are an update of the previous estimates based upon surveys conducted during 1995. In the current analysis, we have accounted for two known sources of bias in the previous surveys associated with the unimodal sighting function and perception. The more recent surveys also included more complete coverage of the management units where fishery mortality rates of bottlenose dolphins are highest.

The current estimates only include dolphins in coastal waters between 0-40 m depth. Bottlenose dolphins associated with the coastal management units may occur inside estuarine waters, and these animals would not be included in the abundance estimates. Likewise, estuarine animals may move into coastal waters very close to shore, and these animals are included in the current estimates. The extent to which coastal and estuarine populations mix or should be considered separate stocks remains unclear. There are resident estuarine groups that are distinct from the coastal animals, but there are also coastal animals that may intermittently or seasonally use estuarine waters. Both the abundance of animals inside estuaries and the movements between the coastal and estuarine habitats are the subject of ongoing study.

The relative distribution of coastal vs. offshore morphotype bottlenose dolphins remains a significant source of uncertainty and potential bias in the current analysis. In particular, during winter months sample sizes are small, there are significant latitudinal gaps in sampling, and samples were collected in localized areas. The validity and robustness of the logistic regression models for winter months remain questionable at this time. The high degree of uncertainty in the models likely imparts a negative bias on the abundance estimates in areas where the predicted probabilities are close to 1. Because the confidence bounds of predicted values is asymmetric in these ranges, there will be a tendency for random samples to be below the predicted value. Since sample sizes are small, additional information may have a large impact on the shape of the curve and the resulting inferences about the relative proportion of the two morphotypes at a given spatial location. This is particularly the case in the winter North Carolina management unit where the current model predicts that a very high proportion of the animals between Cape Hatteras and Cape Lookout are of the coastal morphotype. Additional biopsy samples collected

in this region during January-February are necessary to improve both the accuracy and precision of the current abundance estimates.

The current results reflect an improvement over previous estimates because they are a more recent abundance estimate, account for several known sources of bias, incorporate information on the relative distribution of the two morphotypes, and account for sources of uncertainty. However, several sources of potential positive or negative bias remain, and these are the focus of this continuing research program.

IX. Acknowledgements

We would like to acknowledge the work and dedication of the numerous researchers, observers, vessel staff, and flight crews who participated in the collection of the samples and data that supported this analysis. This work is only the most recent step in an ongoing project within NOAA fisheries to assess the population status and promote prudent management decisions to recover bottlenose dolphin populations on the U.S. east coast. The lead author is indebted to the work of many others who have invested years of time in this effort.

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Table 1. Analysis of deviance results for GAM model for the northern migratory management unit during summer. DF indicates residual degrees of freedom for the model. ΔDev and ΔDf indicate the change in deviance and degrees of freedom respectively for addition of model terms. ns(Factor, 3) indicates fitting a natural cubic spline function with 3 degrees of freedom for each explanatory variable.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ²(ΔDev, ΔDf)
1	NULL	466.733	1181				
2	ns(Depth,3)	395.109	1178	1 - 2	71.624	3	<0.0001***
3	ns(Temp, 3)	461.345	1178	1 - 3	5.388	3	0.1455
4	ns(DFS, 3)	390.158	1178	1 - 4	76.574	3	<0.0001***
5	ns(Depth,3) + ns(DFS, 3)	390.635	1175	4 - 5	4.524	3	0.2102

Table 2. Analysis of deviance results for GAM model for the northern North Carolina management unit during summer. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ²(ΔDev, ΔDf)
1	NULL	138.124	522				
2	ns(Depth,3)	122.410	519	1 - 2	16.002	3	0.0011**
3	ns(Temp, 3)	135.580	519	1 - 3	2.823	3	0.4197
4	ns(DFS, 3)	119.613	519	1 - 4	18.799	3	0.0003**
5	ns(Depth,3) + ns(DFS, 3)	117.810	516	4 - 5	1.803	3	0.6142

Table 3. Analysis of deviance results for GAM model for the southern North Carolina management unit during summer. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ²(ΔDev, ΔDf)
1	NULL	164.889	850				
2	ns(Depth,3)	161.724	847	1 - 2	3.166	3	0.3667
3	ns(Temp, 3)	164.835	847	1 - 3	0.055	3	0.9960
4	ns(DFS, 3)	164.296	847	1 - 4	0.595	3	0.8976

Table 4. Analysis of deviance results for GAM model for the South Carolina management unit during summer. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ²(ΔDev, ΔDf)
1	NULL	185.055	706				
2	ns(Depth,3)	180.275	703	1 - 2	4.779	3	0.1886
3	ns(Temp, 3)	183.765	703	1 - 3	1.290	3	0.7316
4	ns(DFS, 3)	176.974	703	1 - 4	8.081	3	0.0443*
5	ns(Depth,3) + ns(DFS, 3)	176.864	700	4 – 5	0.110	3	0.9906

Table 5. Analysis of deviance results for GAM model for the Georgia management unit during summer. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	191.214	496				
2	ns(Depth,3)	178.614	493	1 - 2	12.626	3	0.0058**
3	ns(Temp, 3)	189.966	493	1 - 3	1.248	3	0.7416
4	ns(DFS, 3)	178.288	493	1 - 4	12.926	3	0.0048**
5	ns(Depth,3) + ns(DFS, 3)	176.284	493	4 - 5	2.004	3	0.5716

Table 6. Analysis of deviance results for GAM model for the northern Florida management unit during summer. Abbreviations as in Table 1. lin(DFS) indicates a linear model for DFS.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	34.208	148				
2	ns(Depth,3)	24.688	145	1 - 2	9.520	3	0.0232*
3	ns(Temp, 3)	25.562	145	1 - 3	8.646	3	0.0344*
4	ns(DFS, 3)	22.114	145	1 - 4	12.094	3	0.0071**
5	ns(Depth,3) + ns(DFS, 3)	19.856	142	4 - 5	2.247	3	0.5226
6	ns(DFS,3) + ns(Temp, 3)	19.449	142	4 - 6	2.665	3	0.5190
7	lin(DFS)	22.724	147	7 - 4	0.610	2	0.7371

Table 7. Analysis of deviance results for GAM model for the central Florida management unit during summer. Abbreviations as in Table 1. lin(Depth) indicates a linear model for Depth.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	79.551	205				
2	ns(Depth,3)	62.553	202	1 - 2	16.998	3	0.0007***
3	ns(Temp, 3)	73.132	202	1 - 3	6.419	3	0.0929
4	ns(DFS, 3)	72.284	202	1 - 4	7.268	3	0.0638
5	ns(Depth,3) + ns(DFS, 3)	59.611	199	2 - 5	2.942	3	0.4007
6	ns(Depth, 3) + ns(Temp, 3)	60.303	199	2 - 6	2.251	3	0.5220
7	lin(Depth)	63.329	201	7 - 2	0.776	2	0.6784

Table 8. Analysis of deviance results for GAM model for the winter North Carolina management units. Abbreviations as in Table 1. TempCode is a binary variable equal to 0 for temperatures <9.5 °C and 1 for temperatures >= 9.5° C. TempCode / ns(dfs,3) indicates natural cubic spline model fits nested within values for TempCode.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	852.177	2476				
2	ns(Depth,3)	764.219	2473	1 - 2	87.958	3	< 0.0001***
3	ns(Temp, 3)	829.277	2473	1 - 3	22.947	3	< 0.0001***
4	ns(DFS, 3)	742.561	2473	1 - 4	109.62	3	< 0.0001***
5	ns(Depth,3) + ns(DFS, 3)	740.330	2470	4 - 5	2.231	3	0.5259
6	TempCode / ns(DFS, 3)	718.376	2472	4 - 6	24.185	3	< 0.0001***

Table 9 Analysis of deviance results for GAM model for the winter South Carolina management unit. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	406.687	1380				
2	ns(Depth,3)	375.682	1377	1 - 2	31.004	3	< 0.0001***
3	ns(Temp, 3)	386.144	1377	1 - 3	20.543	3	0.0001***
4	ns(DFS, 3)	380.405	1377	1 - 4	26.615	3	< 0.0001***
5	ns(Depth,3) + ns(DFS, 3)	373.252	1374	2 - 5	2.429	3	0.4881
6	ns(Depth, 3) + ns(Temp, 3)	368.006	1374	2 - 6	7.676	3	0.0532 [†]

Table 10. Analysis of deviance results for GAM model for the winter Georgia management unit. Abbreviations as in Table 1.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	97.356	331				
2	ns(Depth,3)	90.455	328	1 - 2	6.904	3	0.0751
3	ns(Temp, 3)	91.236	328	1 - 3	6.119	3	0.1059
4	ns(DFS, 3)	88.651	328	1 - 4	8.705	3	0.0335*
5	ns(DFS,3) + ns(Depth, 3)	85.742	325	4 - 5	2.936	3	0.4016
6	ns(DFS, 3) + ns(Temp, 3)	86.542	325	4 - 6	2.109	3	0.5501

Table 11. Total number of biopsy sample locations and morphotype identification by management unit from summer sampling efforts 1998-2002.

Management Unit	Coastal	Offshore	Total
Northern Migratory	19	6	16
N. North Carolina	6	11	25
S. North Carolina	6	18	23
South Carolina	6	7	17
Georgia	3	13	13
North Florida	1	22	24
TOTAL	41	77	118

Table 12. Total number of biopsy sample locations and morphotype identification by management unit for samples collected between October 26, 2001 and March 29, 2002.

Management Unit	Coastal	Offshore	Total
North Carolina	21	5	26
South Carolina	0	1	1
Georgia	13	4	17
TOTAL	44	10	54

Table 13. Analysis of deviance model selection for summer distribution of bottlenose dolphin morphotypes in the southern region.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	78.227	75				
2	Depth	39.529	74	1 - 2	38.698	1	<0.0001***
3	DFS	47.206	74	1 - 3	31.021	1	<0.0001***
4	Temperature	73.229	74	1 - 4	4.998	1	0.0254*
5	Depth + Temperature	39.298	73	2 - 5	0.231	1	0.6308
6	Depth + DFS	36.962	73	2 - 6	2.567	1	0.1091

Table 14. Analysis of maximum likelihood estimates and regression coefficients for summer biopsy samples in the southern region.

Parameter	d.f.	Estimate	Standard Error	Chi-Square	Pr > χ^2	Odds Ratio	Odds Ratio 95 % CI
Intercept	1	2.7653	0.9884	7.8270	0.0051		
Depth	1	-0.1872	0.0523	12.8282	0.0003	0.829	0.748 – 0.919

Table 15. Analysis of deviance model selection for distribution of bottlenose dolphin morphotypes in the North Carolina winter management unit. No valid model fit was possible for the explanatory factor depth.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	25.457	25				
2	DFS	12.066	24	1 - 2	13.311	1	<0.0001***
3	Temperature	10.515	24	1 - 3	14.942	1	<0.0001***
4	Temperature + DFS	8.066	23	3 - 4	2.449	1	0.1176

Table 16. Analysis of maximum likelihood estimates and regression coefficients for winter biopsy samples in the North Carolina management units.

Parameter	d.f.	Estimate	Standard Error	Chi-Square	Pr > χ^2	Odds Ratio	Odds Ratio 95 % CI
Intercept	1	18.3980	9.3446	3.8764	0.0490		
Temperature	1	-0.9238	0.5057	3.3367	0.0678	0.397	0.147 - 1.070

Table 17. Analysis of deviance model selection for distribution of bottlenose dolphin morphotypes in the Georgia winter management unit.   No valid model fit was possible for the two term model containing depth and DFS.

#	Model	Deviance	DF	Comparison	ΔDev	ΔDf	p χ^2(ΔDev, ΔDf)
1	NULL	21.27	17				
2	DFS	11.079	16	1 - 2	10.191	1	0.0014***
3	Temperature	10.529	16	1 - 3	10.741	1	0.0010***
4	Depth	9.051	16	1 - 4	12.219	1	0.0005***
5	Depth + Temperature	9.048	16	4 - 5	0.003	1	0.9563

Table 18. Analysis of maximum likelihood estimates and regression coefficients for winter biopsy samples in the Georgia management unit.

Parameter	d.f.	Estimate	Standard Error	Chi-Square	Pr > χ^2	Odds Ratio	Odds Ratio 95 % CI
Intercept	1	4.2446	1.8002	5.5592	0.0184		
Depth	1	-0.1621	0.0705	5.2836	0.0215	0.850	0.741 – 0.976

Table 19. Survey effort and strata areas during summer 2002 aerial line transect survey.

Management Unit	0-20 m Stratum			20 – 40 m Stratum		
	Survey Effort (km)	Stratum Area (km²)	Number of Groups	Survey Effort (km)	Stratum Area (km²)	Number of Groups
Northern Migratory	1,111.1	8,425	66	878.5	20,966	5
N. North Carolina	411.0	2,787	16	419.7	10,099	4
S. North Carolina	972.6	8,405	18	370.9	14,883	4
South Carolina	732.6	8,373	19	249.4	8,658	9
Georgia	519.7	6,598	24	182.3	7,818	5
Northern Florida	147.0	2,985	4			
Central Florida	249.7	4,547	11			

Table 20. Abundance estimates during the summer 2002 aerial survey based on sightings by team 1. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 280.52 m (%CV = 6.28).

Shallow Stratum 0-20 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density $N\ km^{-2}$	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	54.16	8.19	19.08	3.19	1.677	0.418	14127.4	25.0
N. North Carolina	10.02	3.63	11.77	3.99	0.511	0.232	1424.1	45.4
S. North Carolina	12.01	2.86	15.51	6.16	0.347	0.167	2917.0	48.0
South Carolina	16.97	3.61	10.18	2.27	0.421	0.127	3525.5	30.3
Georgia	14.06	3.80	20.44	10.16	0.996	0.554	6572.1	55.6
Northern Florida	1.02	0.95	1.32	0.95	0.026	0.025	76.8	98.2
Central Florida	5.99	3.09	3.78	1.35	0.166	0.098	756.0	59.2

Deep Stratum 20-40 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density $N\ km^{-2}$	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	1.91	1.33	7.28	3.88	0.033	0.025	689.8	74.8
N. North Carolina	2.99	2.14	21.67	11.57	0.353	0.306	3563.1	86.7
S. North Carolina	2.02	1.35	4.94	3.02	0.053	0.039	787.3	74.6
South Carolina	6.07	1.89	7.08	2.67	0.314	0.149	2715.4	47.6
Georgia	5.08	2.58	9.23	4.02	0.534	0.376	4176.8	70.3

Table 21. Abundance estimates during the summer 2002 aerial survey based on sightings by team 2. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 283.38 m (%CV = 5.79).

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
Shallow Stratum 0-20 m								
Northern Migratory	54.03	7.57	22.00	3.23	1.900	0.393	16008.2	20.7
N. North Carolina	12.99	3.49	18.04	5.96	1.018	0.418	2836.8	41.1
S. North Carolina	11.95	2.74	10.32	6.12	0.228	0.148	1912.7	64.8
South Carolina	13.84	3.52	8.34	1.87	0.282	0.103	2359.9	36.6
Georgia	21.97	4.83	7.73	1.42	0.578	0.164	3813.9	28.4
Northern Florida	4.05	2.88	4.85	1.66	0.276	0.212	822.5	76.8
Central Florida	10.00	3.50	3.06	0.93	0.216	0.096	982.0	44.5
Deep Stratum 20-40 m								
Northern Migratory	4.99	2.16	6.80	1.71	0.068	0.032	1429.9	46.7
N. North Carolina	3.99	2.33	17.59	9.87	0.357	0.301	3604.6	84.4
S. North Carolina	4.01	1.82	4.98	1.82	0.095	0.051	1421.0	53.0
South Carolina	8.08	2.44	5.52	1.47	0.333	0.154	2885.7	46.2
Georgia	5.08	2.58	9.23	4.02	0.529	0.371	4135.1	70.2

Table 22. Abundance estimates during the summer 2002 aerial survey based on sightings by both teams. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 262.72 m (%CV = 6.38).

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density $N\ km^{-2}$	Std. Error Dens.	Abundance	% CV Abundance
Shallow Stratum 0-20 m								
Northern Migratory	42.17	6.94	22.61	3.93	1.647	0.411	13876.3	24.9
N. North Carolina	6.95	2.68	15.87	4.86	0.516	0.244	1438.6	47.2
S. North Carolina	5.95	2.14	14.54	11.82	0.173	0.152	1455.5	87.6
South Carolina	11.88	3.32	9.36	1.88	0.294	0.112	2460.4	38.0
Georgia	12.03	3.76	10.48	2.94	0.454	0.164	2992.2	36.1
Northern Florida	1.02	0.95	1.32	0.95	0.027	0.027	82.0	98.3
Central Florida	4.98	2.27	4.09	1.45	0.162	0.094	738.5	57.8
Deep Stratum 20-40 m								
Northern Migratory	1.91	1.33	7.28	3.88	0.035	0.026	736.2	74.8
N. North Carolina	2.99	2.14	21.63	11.58	0.376	0.327	3798.8	86.9
S. North Carolina	2.02	1.35	4.94	3.02	0.057	0.042	841.7	74.7
South Carolina	5.06	1.67	7.12	3.26	0.281	0.149	2428.7	53.1
Georgia	5.08	2.58	9.23	4.02	0.570	0.401	4459.5	70.3

Table 23. Abundance estimates corrected for perception bias during the summer 2002 aerial survey. $g(d_{max})$ indicates the visibility bias correction of density estimates for respective observer teams.

Management Unit	Density N km^{-2}	Std Error Density	Team 1 $g(d_{max})$	SE Team 1 $g(d_{max})$	Team 2 $g(d_{max})$	SE Team2 $g(d_{max})$	Abundance	% CV Abundance
Shallow Stratum 0-20 m								
Northern Migratory	1.935	0.402	0.86	0.09	0.983	0.045	16301.5	20.8
N. North Carolina	1.026	0.436	0.54	0.23	1.015	0.560	2860.1	42.5
S. North Carolina	0.664	0.554	0.64	0.29	0.434	0.269	5578.6	83.5
South Carolina	0.405	0.118	1.04	0.06	0.703	0.186	3391.4	29.1
Georgia	1.297	0.721	0.77	0.12	0.581	0.297	8555.9	55.6
Northern Florida	0.359	0.167	0.11	0.02	1.068	0.032	1071.3	46.6
Central Florida	0.223	0.102	0.72	0.20	0.992	0.064	1012.1	45.9
Deep Stratum 20-40 m								
Northern Migratory	0.069	0.028	0.57	0.23	1.068	0.032	1446.2	40.9
N. North Carolina	0.381	0.272	1.04	0.08	1.068	0.031	3844.1	71.4
S. North Carolina	0.095	0.046	0.64	0.27	1.068	0.031	1416.1	48.1
South Carolina	0.378	0.154	0.82	0.17	0.882	0.181	3274.3	40.7
Georgia	0.505	0.345	1.08	0.04	1.068	0.032	3944.2	68.3

Table 24. Survey effort and strata areas during winter 2002 aerial line transect survey.

Management Unit	0-20 m Stratum			20 – 40 m Stratum		
	Survey Effort (km)	Stratum Area (km^2)	Number of Groups	Survey Effort (km)	Stratum Area (km^2)	Number of Groups
North Carolina	2014.2	11247	84	1892.0	26575	27
South Carolina	1426.67	8373	43	620.6	8658	16
Georgia	459.1	6598	15		7818	

Table 25. Abundance estimates during the winter 2002 aerial survey based on sightings by team 1. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 273.13 m (%CV = 5.32).

Shallow Stratum 0-20 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	70.74	13.38	18.93	2.66	1.237	0.349	13915.5	28.2
South Carolina	33.14	6.48	4.18	0.51	0.179	0.043	1498.5	24.0
Georgia	7.86	2.45	5.96	1.36	0.193	0.085	1276.1	43.9

Deep Stratum 20-40 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	22.08	5.65	8.04	1.74	0.171	0.053	4544.3	31.2
South Carolina	11.11	4.19	6.93	1.91	0.236	0.125	2046.5	52.8

Table 26. Abundance estimates during the winter 2002 aerial survey based on sightings by team 2. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 275.82 m (%CV = 5.09).

Shallow Stratum 0-20 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	72.82	13.37	20.22	2.71	1.351	0.383	15190.3	28.4
South Carolina	35.01	7.16	4.21	0.51	0.188	0.045	1572.6	23.7
Georgia	12.95	3.61	5.69	0.91	0.292	0.095	1926.9	32.4

Deep Stratum 20-40 m

Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	25.14	6.48	7.58	1.49	0.182	0.054	4824.5	29.7
South Carolina	13.02	5.51	6.66	1.85	0.261	0.142	2259.6	54.6

Table 27. Abundance estimates during the winter 2002 aerial survey based on sightings by both teams. Mean and standard errors of the bootstrap distribution for each parameter are shown. Estimated Effective Strip Width (ESW) = 260.42 m (%CV = 5.10).

Shallow Stratum 0-20 m								
Management Unit	Mean # Groups	Std Error # Groups	Mean Group Size	Std. Err. Group Size	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	61.75	12.25	20.90	2.80	1.252	0.362	14082.9	28.9
South Carolina	25.09	5.58	4.49	0.68	0.152	0.041	1275.1	27.0
Georgia	5.84	2.54	6.79	1.61	0.172	0.088	1134.5	51.2
Deep Stratum 20-40 m								
North Carolina	21.08	5.63	8.39	1.80	0.178	0.056	4740.0	31.5
South Carolina	10.09	4.22	7.34	2.07	0.238	0.132	2063.2	55.3

Table 28. Abundance estimates corrected for perception bias during the winter 2002 aerial survey. g(d$_{max}$) indicates the visibility bias correction of density estimates for respective observer teams.

Shallow Stratum 0-20 m							
Management Unit	Density N km^{-2}	Std Error Density	Team 1 g(d$_{max}$)	SE Team 1 g(d$_{max}$)	Team 2 g(d$_{max}$)	SE Team 2 g(d$_{max}$)	Abundance	% CV Abundance
North Carolina	1.334	0.369	0.93	0.05	1.010	0.034	15008.4	27.6
South Carolina	0.222	0.050	0.81	0.09	0.847	0.076	1857.8	22.5
Georgia	0.341	0.102	0.58	0.20	0.872	0.170	2251.2	29.8
Deep Stratum 20-40 m							
North Carolina	0.174	0.051	0.98	0.05	1.042	0.028	4625.9	29.4
South Carolina	0.259	0.135	0.91	0.08	0.991	0.090	2243.1	52.0

Table 29. Abundance estimates of the coastal morphotype during summer 2002 aerial survey based on sightings by team 1. Mean and standard errors of the bootstrap distribution for each parameter are shown.

Shallow Stratum 0-20 m						
Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	1057.12	242.54	1.705	0.402	14368.5	23.6
N. North Carolina	118.34	52.53	0.518	0.229	1442.3	44.3
S. North Carolina	109.51	51.33	0.201	0.095	1693.4	47.3
South Carolina	96.90	31.97	0.238	0.081	1990.7	34.2
Georgia	185.55	96.23	0.645	0.351	4256.7	54.4
Northern Florida	1.06	1.03	0.013	0.014	40.1	101.5
Central Florida	18.06	10.58	0.130	0.080	592.8	61.3
Deep Stratum 20-40 m						
Northern Migratory	11.66	12.03	0.024	0.024	493.9	102.4
N. North Carolina	82.17	69.51	0.362	0.313	3653.2	86.7
S. North Carolina	0.93	0.84	0.005	0.004	68.0	89.8
South Carolina	4.71	2.70	0.035	0.022	302.9	61.9
Georgia	7.93	6.21	0.079	0.062	620.5	77.5

Table 30. Abundance estimates of the coastal morphotype during summer 2002 aerial survey based on sightings by team 2. Mean and standard errors of the bootstrap distribution for each parameter are shown.

Shallow Stratum 0-20 m						
Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	1219.08	251.60	1.937	0.384	16316.2	19.8
N. North Carolina	230.75	93.03	1.001	0.413	2788.5	41.3
S. North Carolina	57.47	36.52	0.106	0.069	887.1	65.5
South Carolina	73.14	29.75	0.178	0.075	1486.7	42.1
Georgia	113.66	34.26	0.389	0.124	2563.7	31.9
Northern Florida	14.67	11.66	0.182	0.151	542.7	83.0
Central Florida	21.69	10.04	0.155	0.077	705.3	49.6
Deep Stratum 20-40 m						
Northern Migratory	28.59	15.54	0.057	0.031	1203.3	53.9
N. North Carolina	82.17	69.51	0.356	0.309	3599.8	86.7
S. North Carolina	1.80	1.23	0.009	0.006	132.1	71.0
South Carolina	6.67	3.05	0.049	0.025	424.0	50.5
Georgia	7.93	6.21	0.078	0.061	612.1	77.7

Table 31. Abundance estimates of the coastal morphotype during summer 2002 aerial survey based on sightings by both teams. Mean and standard errors of the bootstrap distribution for each parameter are shown.

Shallow Stratum 0-20 m

Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	976.02	232.18	1.675	0.395	14114.6	23.6
N. North Carolina	112.65	52.20	0.525	0.242	1462.9	46.1
S. North Carolina	41.17	36.20	0.082	0.073	685.6	88.9
South Carolina	71.73	29.79	0.188	0.081	1574.9	43.2
Georgia	82.39	33.63	0.303	0.126	2000.8	41.6
Northern Florida	1.06	1.03	0.014	0.015	42.8	101.7
Central Florida	16.67	9.53	0.129	0.077	584.4	60.0

Deep Stratum 20-40 m

Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
Northern Migratory	11.66	12.03	0.025	0.026	526.8	102.5
N. North Carolina	82.17	69.51	0.386	0.334	3894.5	86.5
S. North Carolina	0.93	0.84	0.005	0.004	72.4	89.4
South Carolina	4.67	2.70	0.037	0.023	320.2	62.2
Georgia	7.93	6.21	0.085	0.066	661.3	77.7

Table 32. Abundance estimates of the coastal morphotype corrected for perception bias during the summer 2002 aerial survey. $g(d_{max})$ indicates the visibility bias correction of density estimates for respective observer teams.

Management Unit	Density N km^{-2}	Std Error Density	Team 1 $g(d_{max})$	SE Team 1 $g(d_{max})$	Team 2 $g(d_{max})$	SE Team 2 $g(d_{max})$	Abundance	% CV Abundance
Shallow Stratum 0-20 m								
Northern Migratory	1.972	0.391	0.86	0.09	0.983	0.046	16610.7	19.8
N. North Carolina	0.999	0.414	0.56	0.23	1.004	0.065	2783.3	41.4
S. North Carolina	0.421	0.481	0.65	0.29	0.374	0.253	3534.3	114.4
South Carolina	0.225	0.074	1.05	0.05	0.779	0.162	1882.2	33.0
Georgia	0.858	0.474	0.76	0.14	0.575	0.291	5660.4	55.2
Northern Florida	0.247	0.116	0.08	0.02	1.066	0.032	736.6	47.0
Central Florida	0.158	0.080	0.78	0.17	0.999	0.058	718.4	50.9
Deep Stratum 20-40 m								
Northern Migratory	0.067	0.026	0.60	0.21	1.067	0.032	1399.9	39.6
N. North Carolina	0.381	0.280	1.08	0.04	1.066	0.032	3850.6	73.3
S. North Carolina	0.009	0.006	0.65	0.30	1.068	0.037	132.4	66.1
South Carolina	0.046	0.023	0.75	0.22	1.056	0.045	401.7	50.0
Georgia	0.075	0.057	1.08	0.05	1.067	0.032	584.3	75.6

Table 33. Mean total estimated abundance of the coastal morphotype between 0-40 m depth by management unit during summer 2002. Estimates are for 0-20 m depth in the central and northern Florida units. Confidence limits are from the bootstrap distribution of 1000 estimates using the percentile method.

Management Unit	Mean Abundance	SE Abundance	% CV	95 % Confidence Interval	Lower Limit 60% CI (Nmin)
Northern Migratory	17466.1	3334.3	19.1	11497.7 – 24956.5	14620.9
N. North Carolina	6160.2	3197.9	51.9	1484.9 – 13399.0	3254.7
S. North Carolina	3645.8	4048.0	111.0	1084.1 – 13135.6	1863.2
South Carolina	2283.5	627.2	27.5	1160.1 – 3701.0	1776.4
Georgia	6234.8	3151.4	50.5	2089.8 – 13388.7	3335.4
Northern Florida	736.6	346.3	47.0	345.1 – 1585.3	454.9
Central Florida	718.4	365.3	50.9	148.7 – 15611.9	402.9

Table 34. Abundance estimates of the coastal morphotype during winter 2002 aerial survey based on sightings by team 1. Mean and standard errors of the bootstrap distribution for each parameter are shown.

Shallow Stratum 0-20 m						
Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	1201.90	296.56	1.097	0.291	12340.9	26.6
South Carolina	126.07	28.50	0.163	0.040	1361.6	24.5
Georgia	42.80	19.59	0.171	0.080	1130.4	46.4
Deep Stratum 20-40 m						
North Carolina	127.71	38.56	0.124	0.040	3296.9	31.9
South Carolina	25.11	18.77	0.074	0.056	638.5	75.3

Table 35. Abundance estimates of the coastal morphotype during winter 2002 aerial survey based on sightings by team 2. Mean and standard errors of the bootstrap distribution for each parameter are shown.

Shallow Stratum 0-20 m						
Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	1340.16	338.18	1.213	0.325	13637.7	26.8
South Carolina	132.76	29.24	0.170	0.041	1422.7	24.2
Georgia	65.59	22.28	0.259	0.089	1712.0	34.5
Deep Stratum 20-40 m						
North Carolina	140.55	41.41	0.135	0.041	3587.9	30.2
South Carolina	28.24	20.25	0.083	0.061	715.8	73.5

Table 36. Abundance estimates of the coastal morphotype during winter 2002 aerial survey based on sightings by both teams. Mean and standard errors of the bootstrap distribution for each parameter are shown

Shallow Stratum 0-20 m						
Management Unit	Mean # Animals	Std Error # Animals	Density N km^{-2}	Std. Error Dens.	Abundance	% CV Abundance
North Carolina	1157.42	295.79	1.110	0.303	12481.2	27.3
South Carolina	102.35	26.52	0.139	0.039	1162.5	27.9
Georgia	36.50	20.04	0.152	0.083	1006.2	54.6
Deep Stratum 20-40 m						
North Carolina	127.30	38.59	0.130	0.041	3451.4	31.9
South Carolina	24.38	18.78	0.075	0.058	651.1	77.6

Table 37. Abundance estimates of the coastal morphotype corrected for perception bias during the winter 2002 aerial survey. $g(d_{max})$ indicates the visibility bias correction of density estimates for respective observer teams.

Shallow Stratum 0-20 m							
Management Unit	Density N km^{-2}	Std Error Density	Team 1 $g(d_{max})$	SE Team 1 $g(d_{max})$	Team 2 $g(d_{max})$	SE Team2 $g(d_{max})$	Abundance	% CV Abundance
North Carolina	1.199	0.313	0.92	0.05	1.329	0.363	13485.5	26.1
South Carolina	0.200	0.045	0.81	0.09	0.210	0.052	1675.3	22.4
Georgia	0.305	0.102	0.57	0.20	0.528	0.355	2012.5	33.3
Deep Stratum 20-40 m							
North Carolina	0.129	0.039	0.96	0.06	0.141	0.042	3427.5	30.3
South Carolina	0.081	0.058	0.89	0.12	0.092	0.065	703.6	71.0

Table 38. Mean total estimated abundance of the coastal morphotype between 0-40 m depth by management unit during winter 2002. Only the 0-20 m depth stratum is included in the Georgia management unit. Confidence limits are from the bootstrap distribution of 1000 estimates using the percentile method.

Management Unit	Mean Abundance	SE Abundance	% CV	95 % Confidence Interval	Lower Limit 60% CI (Nmin)
North Carolina	16913	3887.1	23.0	10230.3 –25512.5	13558.4
South Carolina	2378.3	715.0	30.1	1348.0 – 4284.4	1815.8
Georgia	2012.5	670.1	33.3	925.0 – 3471.9	1497.1

Figure 1. Coastal morphotype bottlenose dolphin management units identified in recent stock assessment (NMFS 2001).
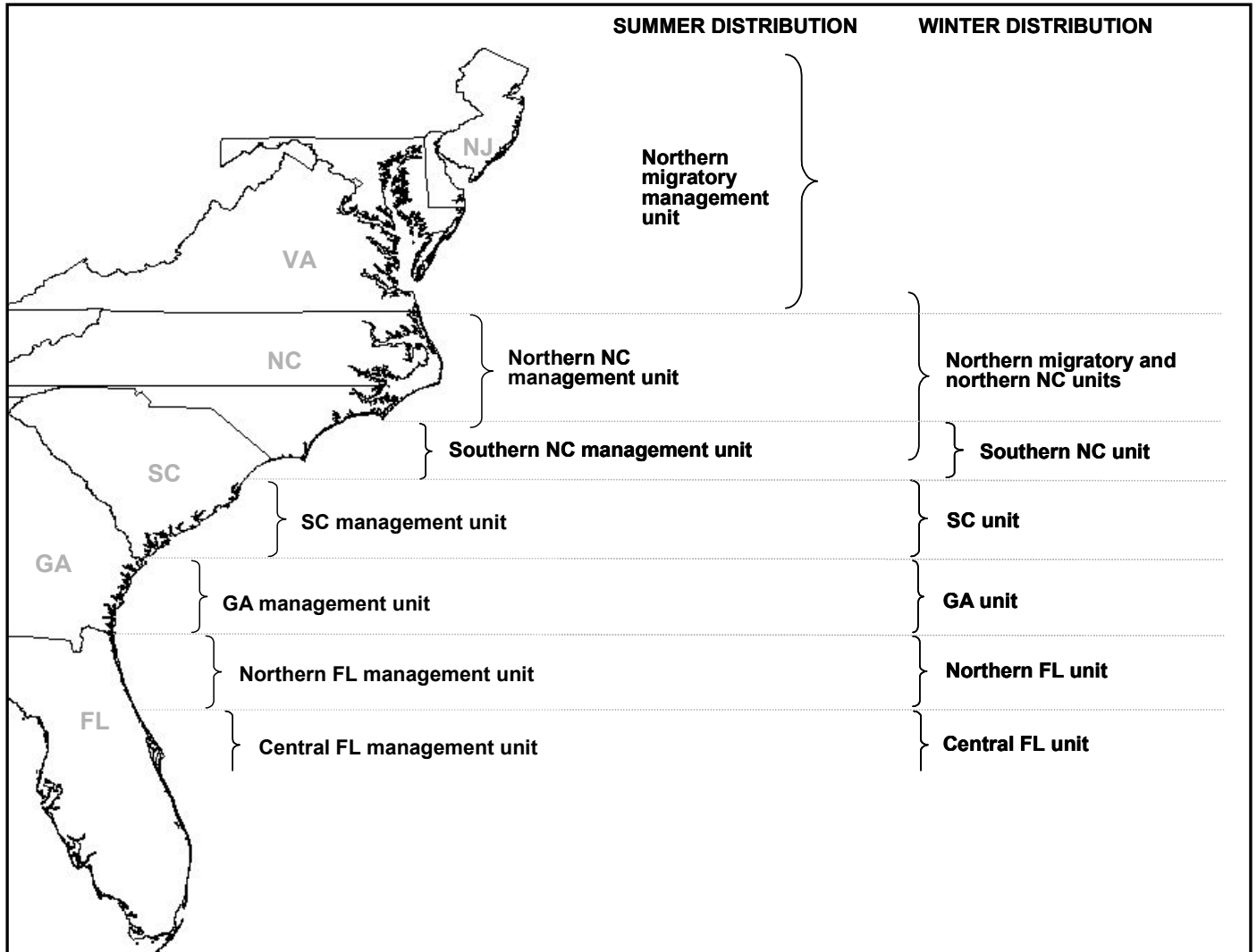
Figure 2. Winter 2002 aerial survey transect lines and bottlenose dolphin sightings. Light gray area indications shallow water stratum (0-20 m depth), and dark gray indicates offshore stratum (20-40 m depth). Management unit boundaries are indicated by dotted lines.
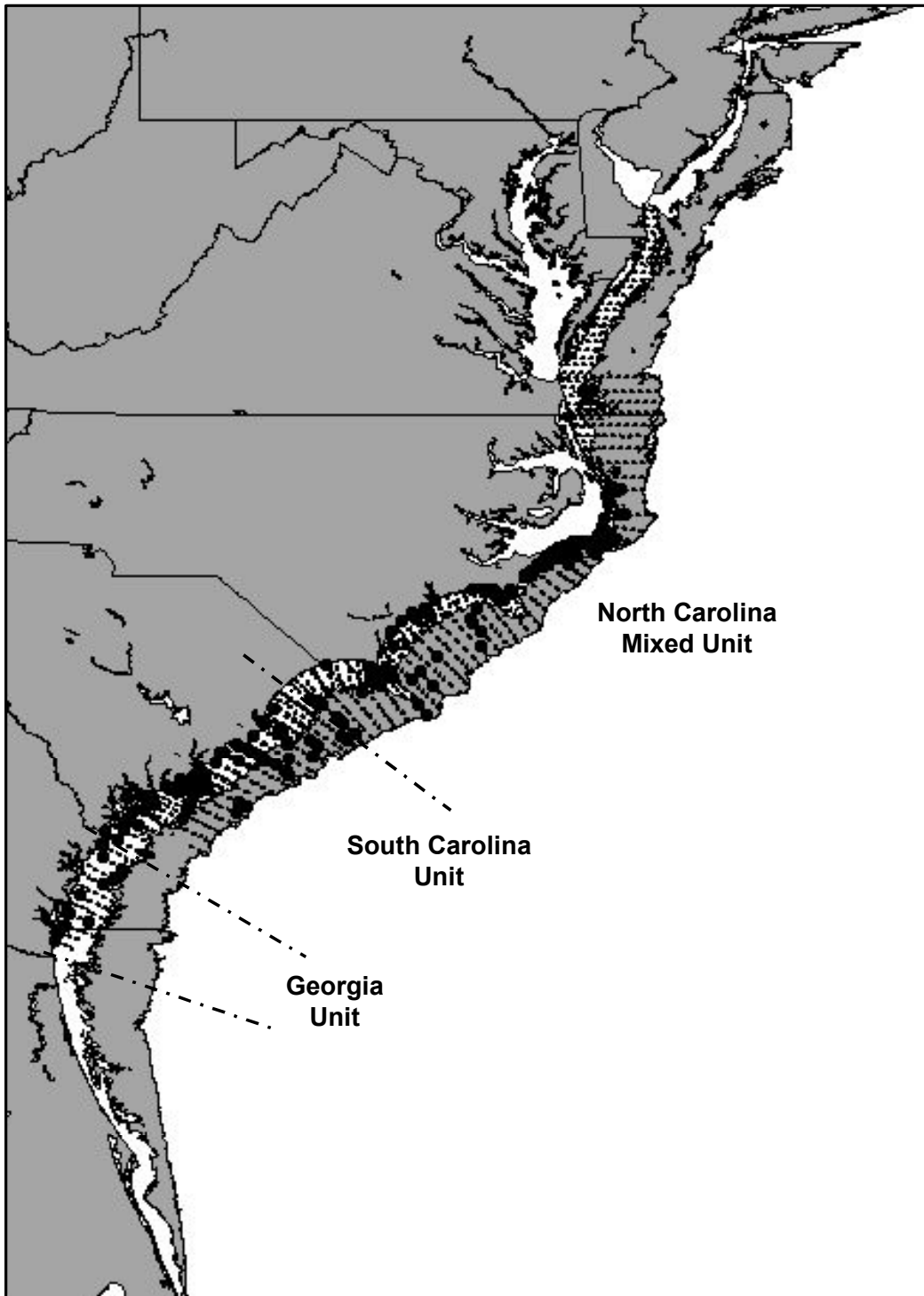
Figure 3. Summer 2002 aerial survey transect lines. Light gray area indicates shallow water stratum (0-20 m depth), and dark gray indicates offshore stratum (20-40 m depth). Management unit boundaries are indicated by dotted lines.
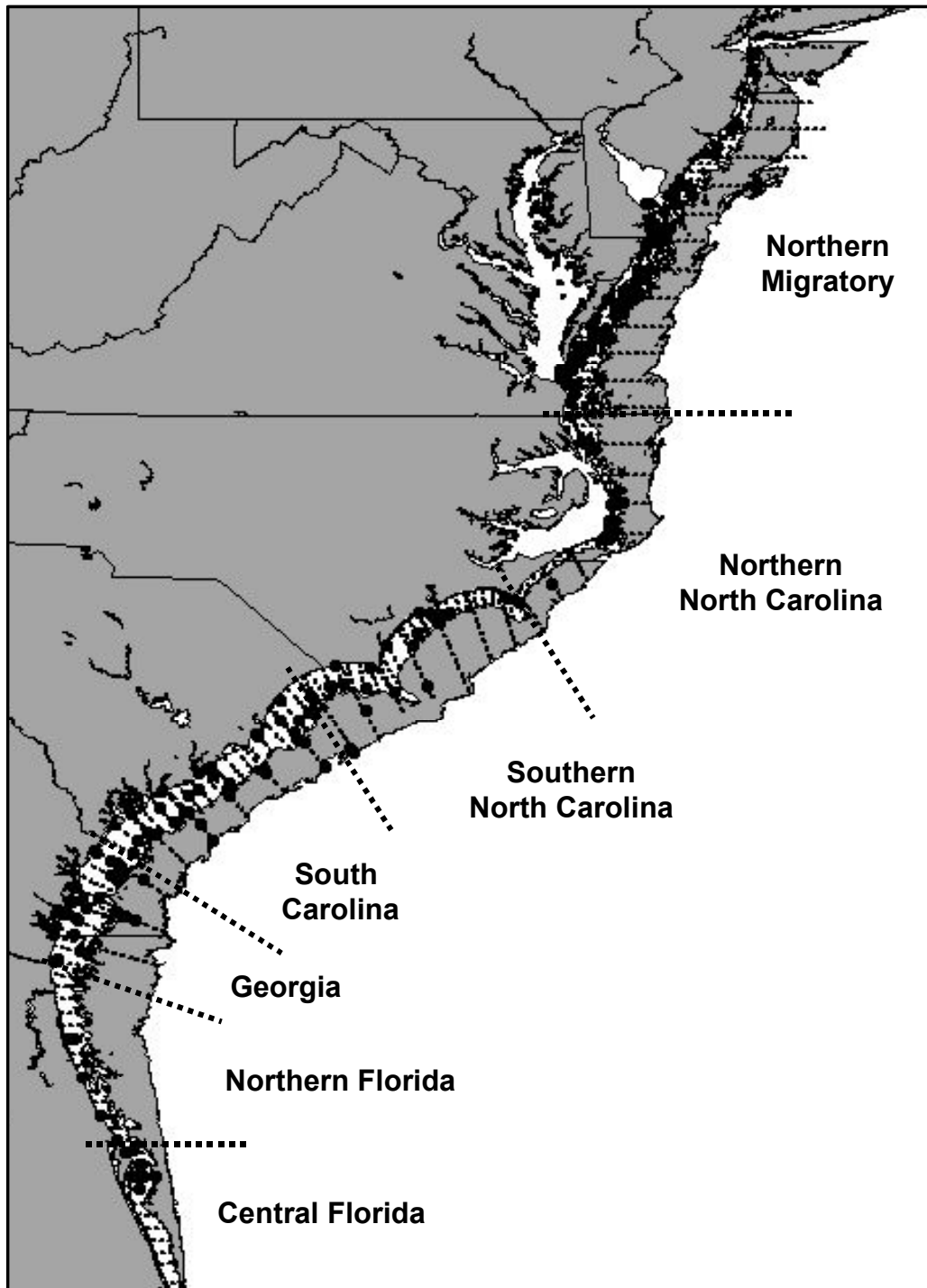
Figure 4. Observer team configuration inside NOAA Twin Otter during aerial survey procedures.
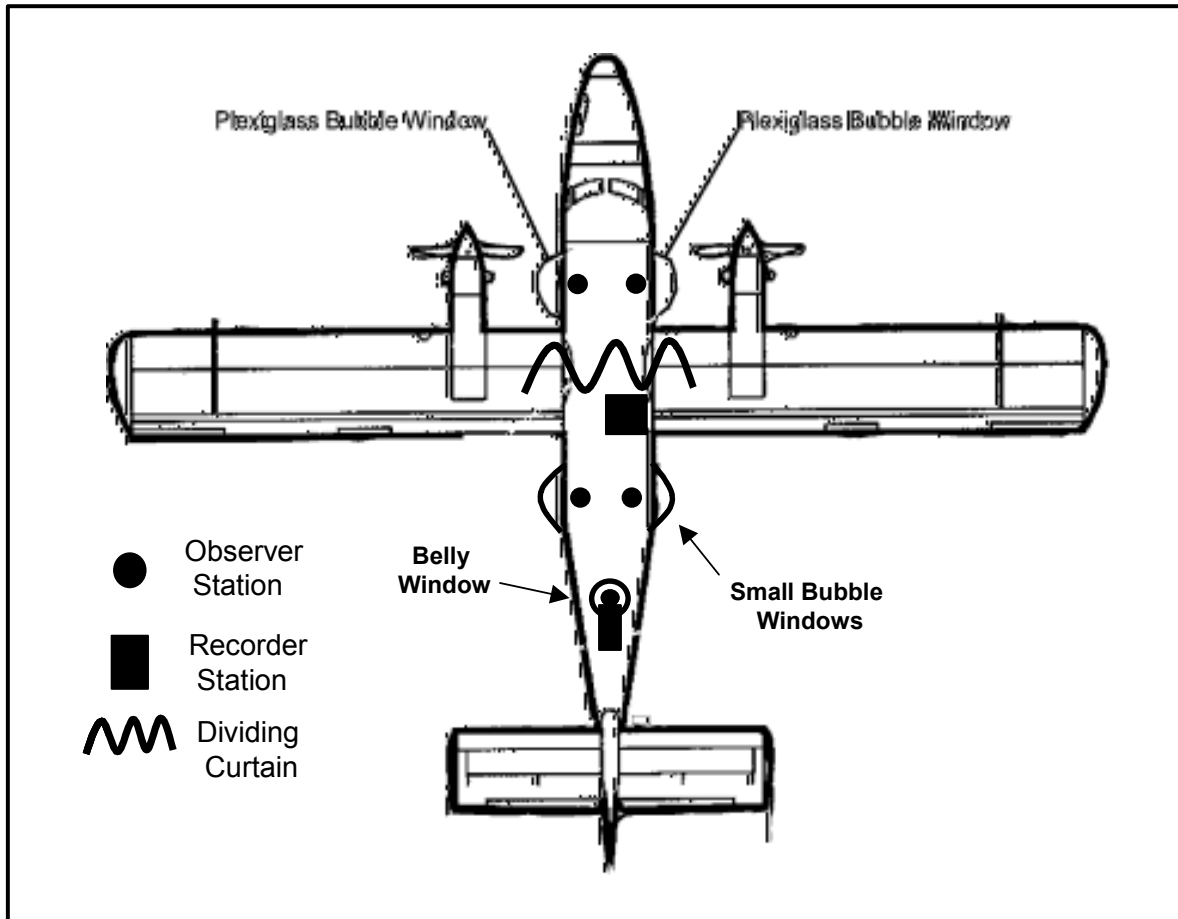
Figure 5. Survey tracklines for large vessel surveys of the Atlantic during summer 1998 and 1999 and winter 2002. Locations of biopsy samples from bottlenose dolphins are indicated.
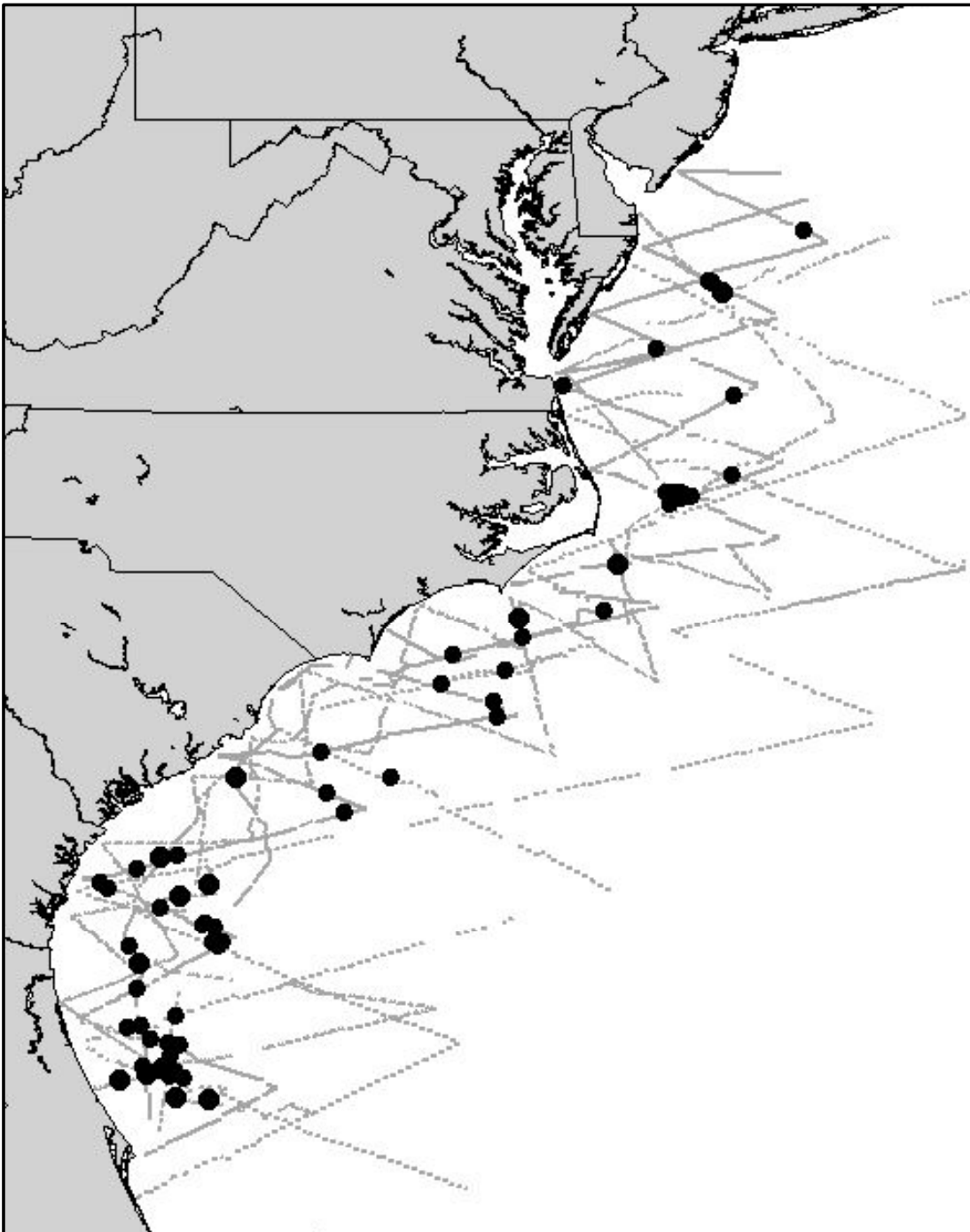
Figure 6. Completed tracklines during summer 2001 small vessel biopsy survey. Locations of biopsy samples from bottlenose dolphins are indicated. Sampling regions and strata boundaries are shown.
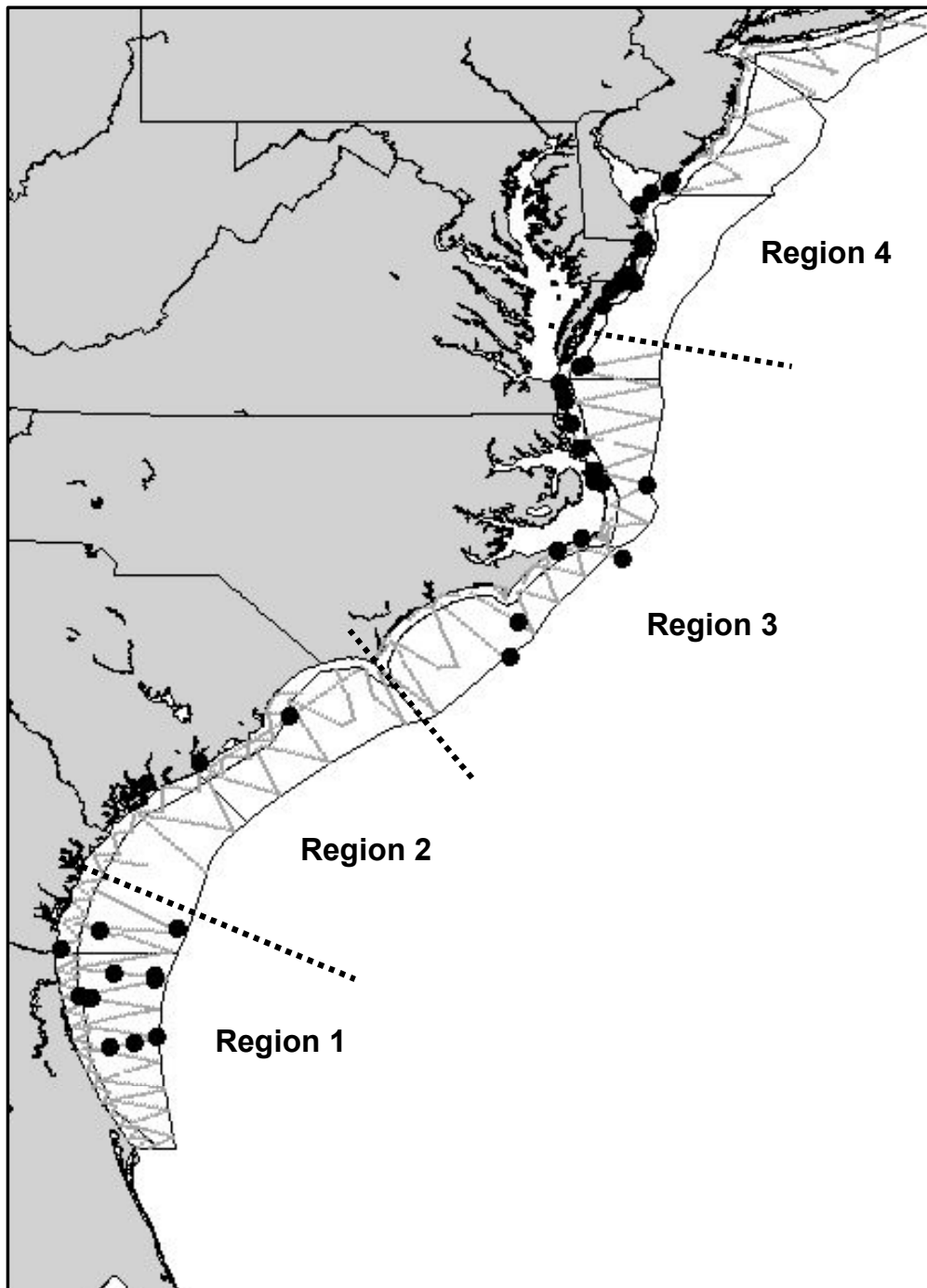
Figure 7. Operational areas and during summer 2002 biopsy survey. Locations of biopsy samples from bottlenose dolphins are indicated.
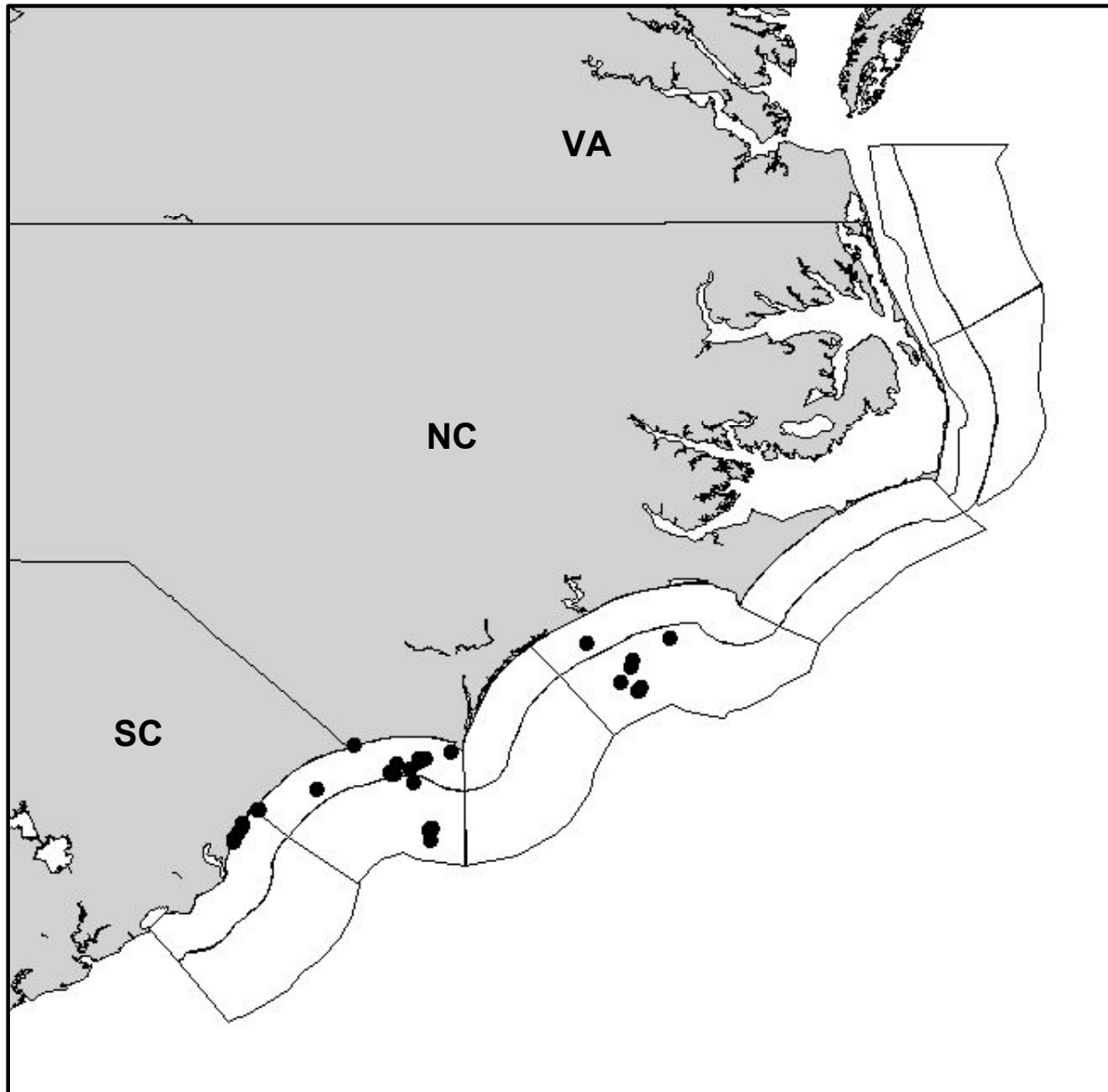
Figure 8. Locations of collected biopsy samples in local sample collections during winter 2002.
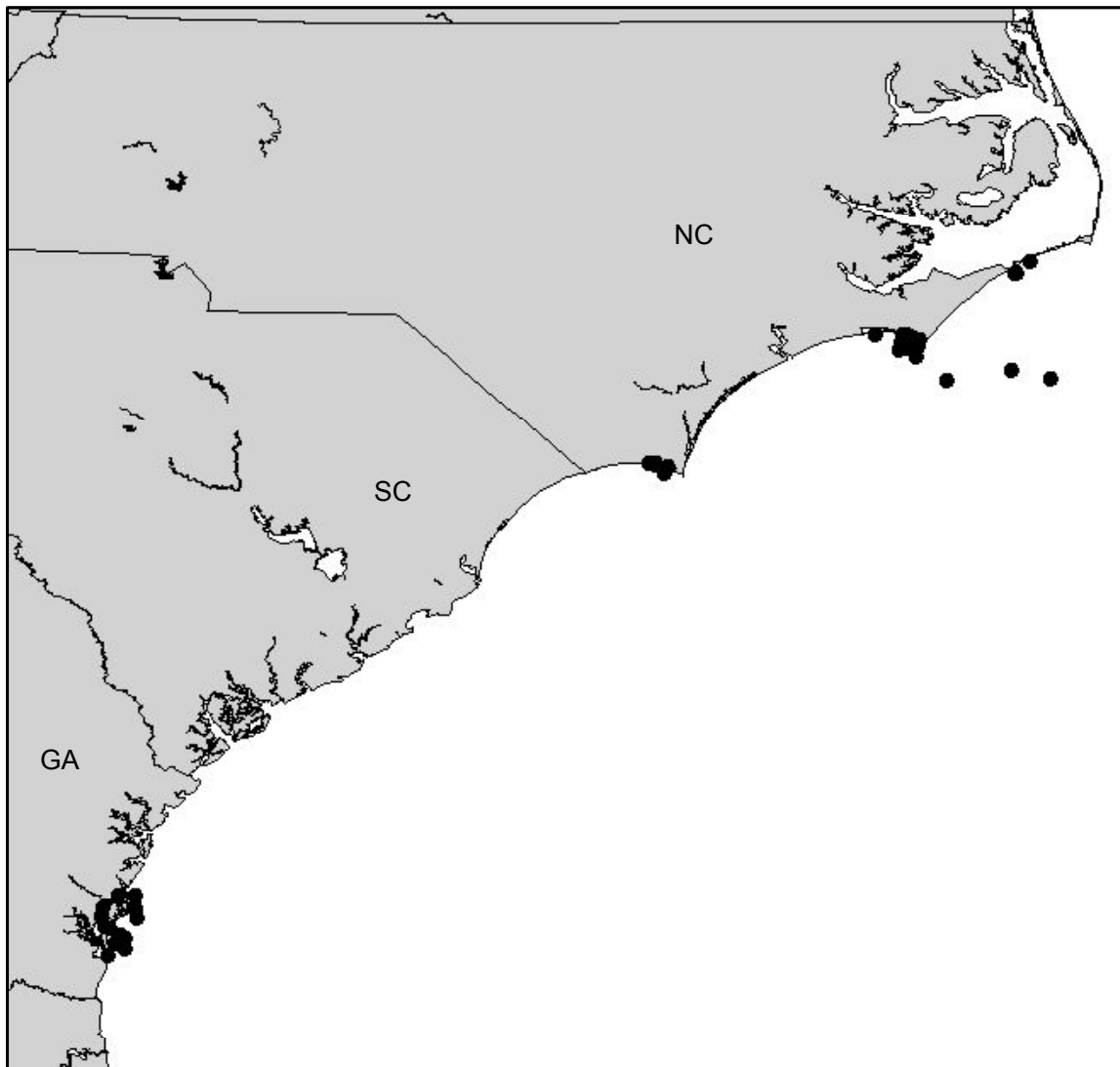
Figure 9. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer northern migratory management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
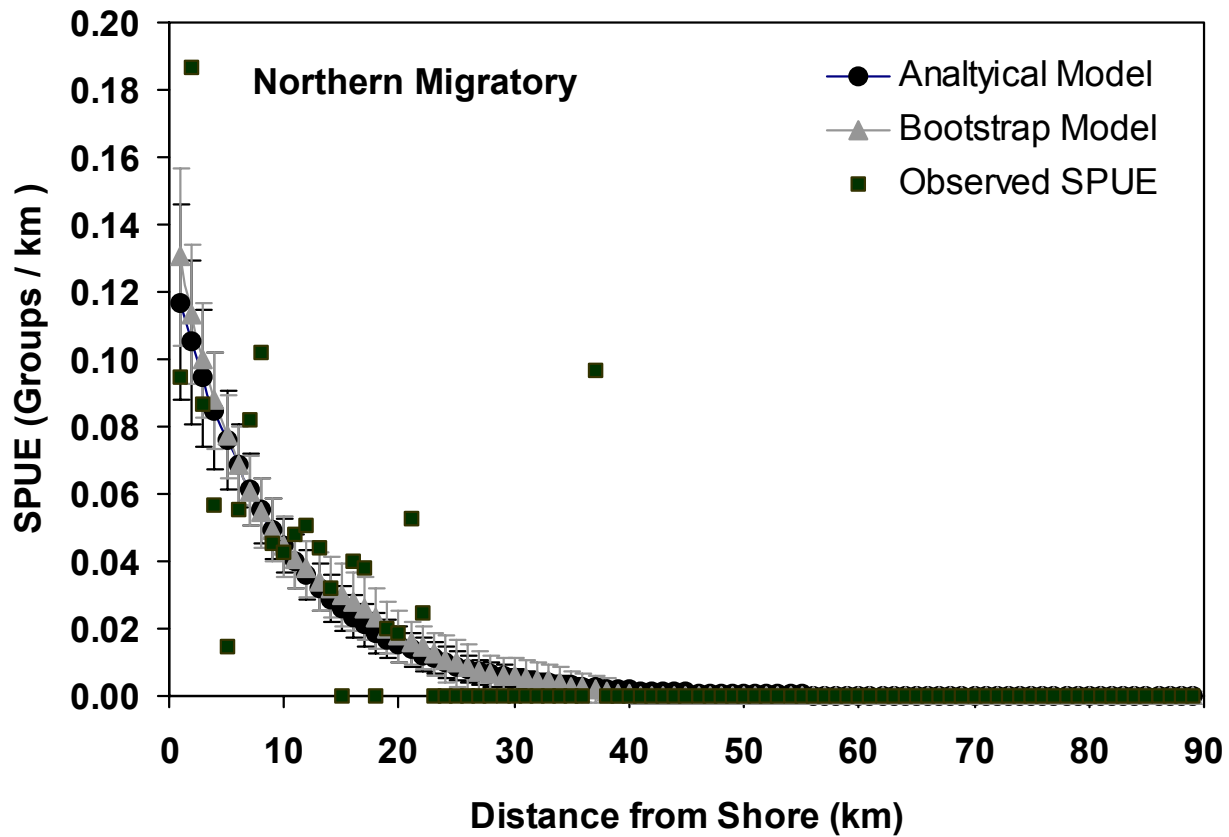
Figure 10. Number of animals per bottlenose dolphin groups during summer as a function of distance from shore in the (A) northern migratory and (B) northern North Carolina management units.
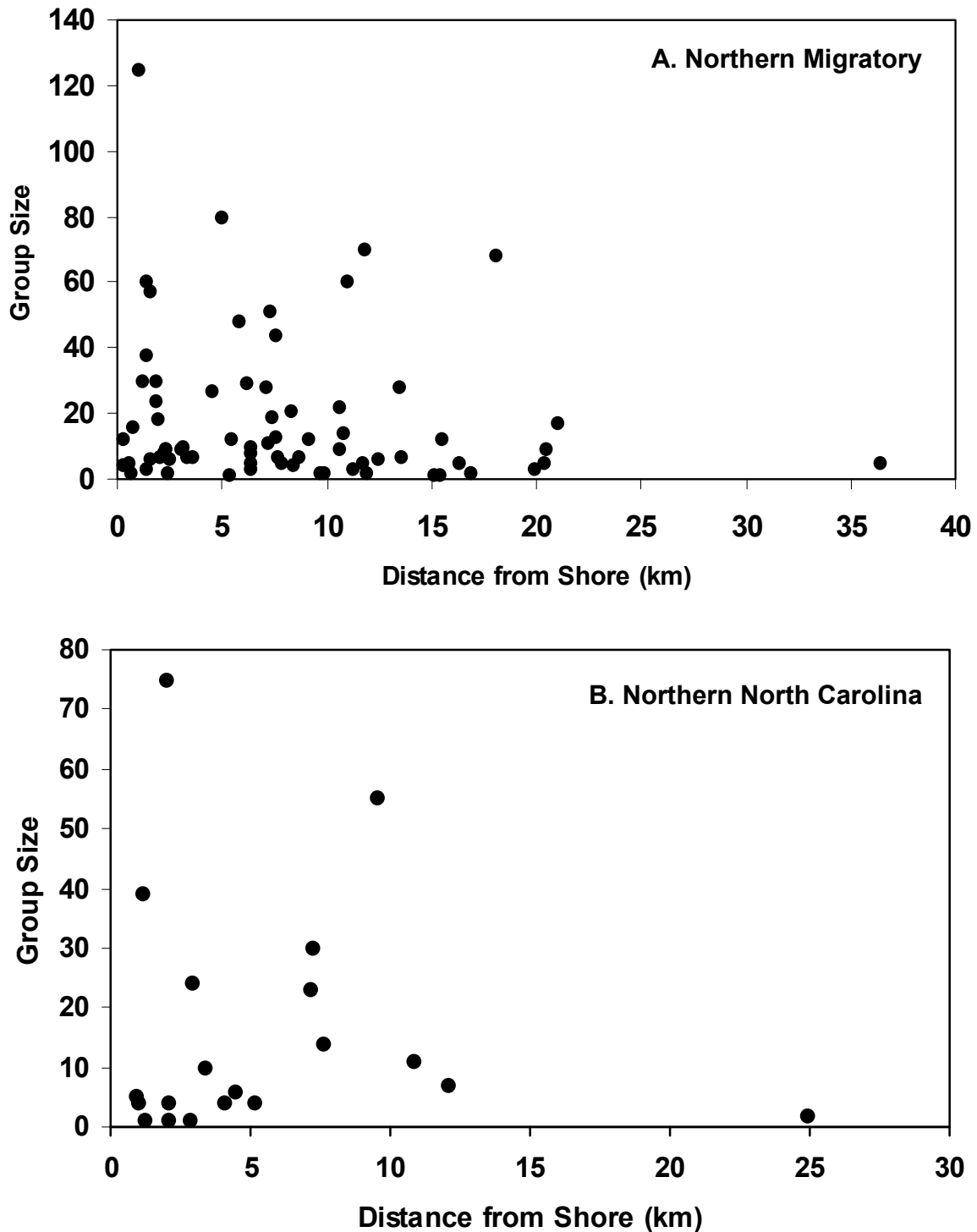
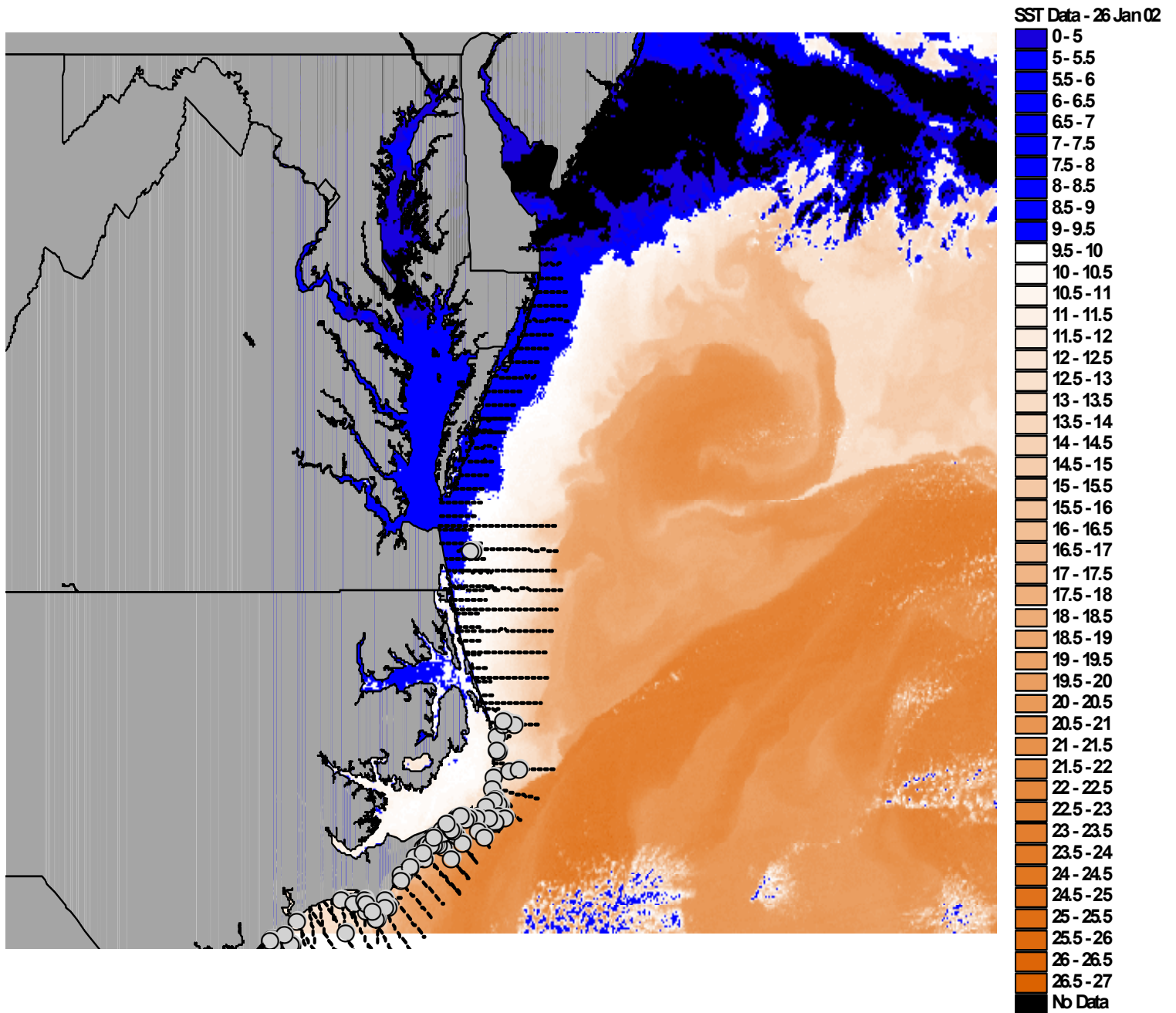**Figure 11.** Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer northern North Carolina management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
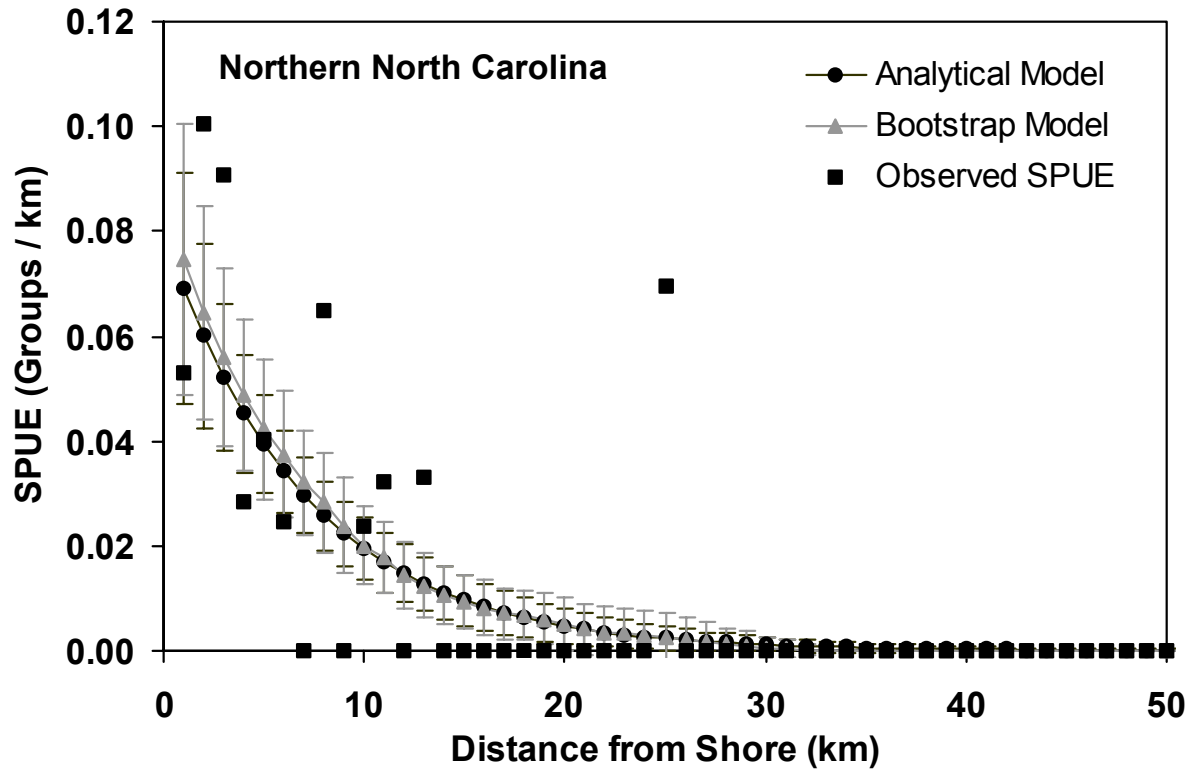
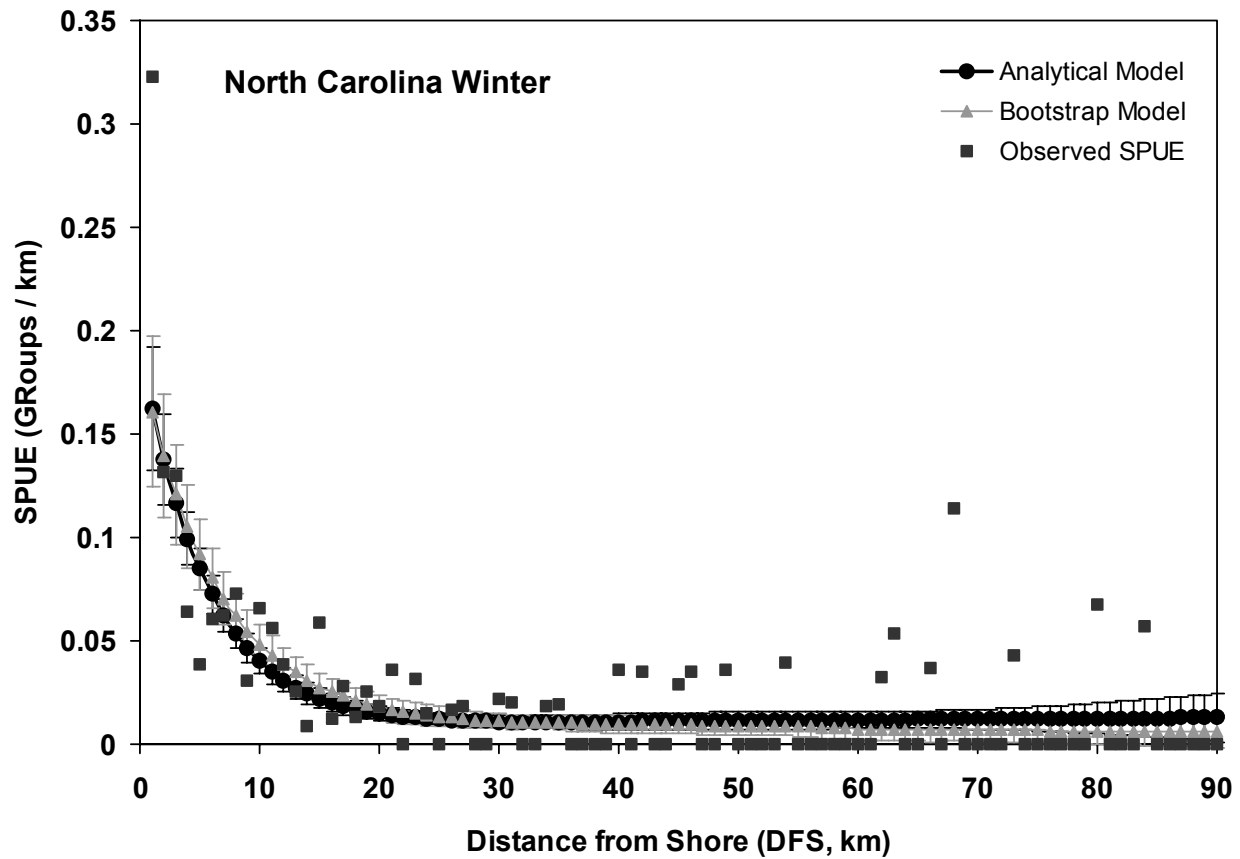**Figure 12.** Observed SPUE values in 1 km distance from shore intervals for the southern North Carolina management unit during summer.
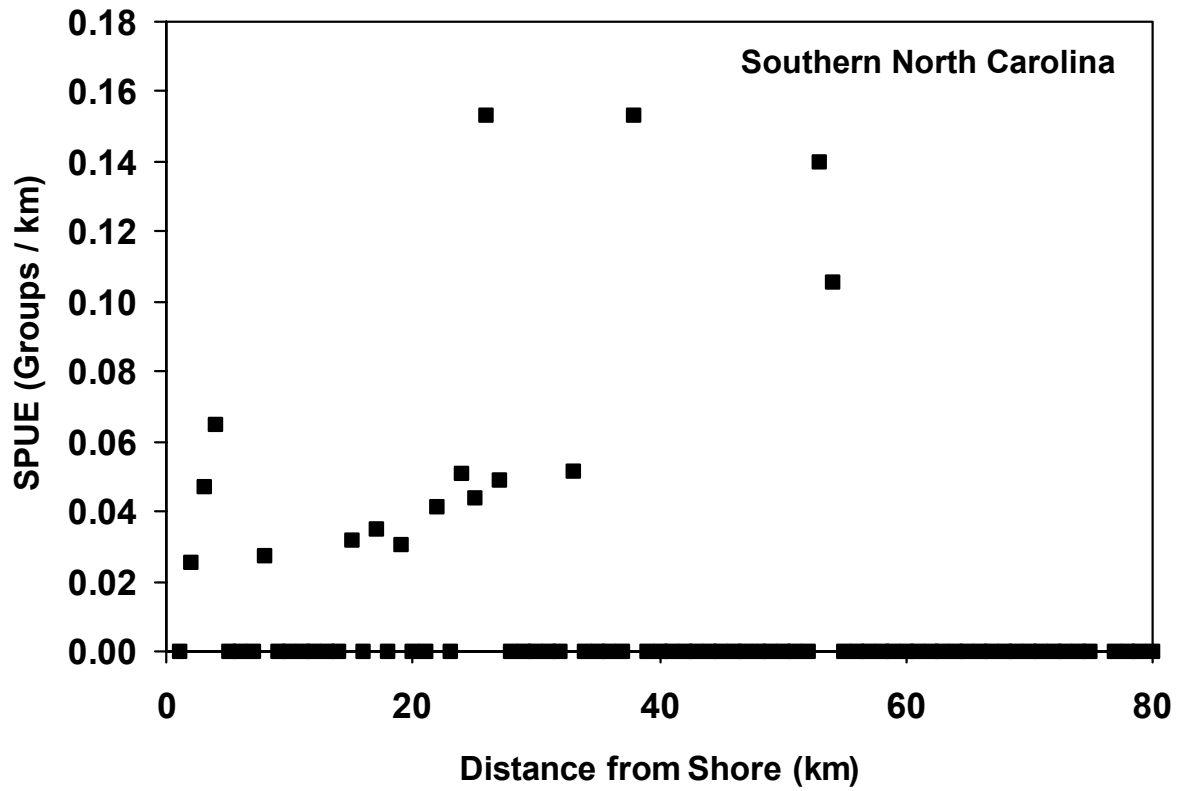
Figure 13. Number of animals per bottlenose dolphin groups during summer as a function of distance from shore in the (A) southern North Carolina, (B) South Carolina, and (C) Georgia management units. The fitted curve from a marginally non-significant regression against log(Group Size) is shown for South Carolina (B).
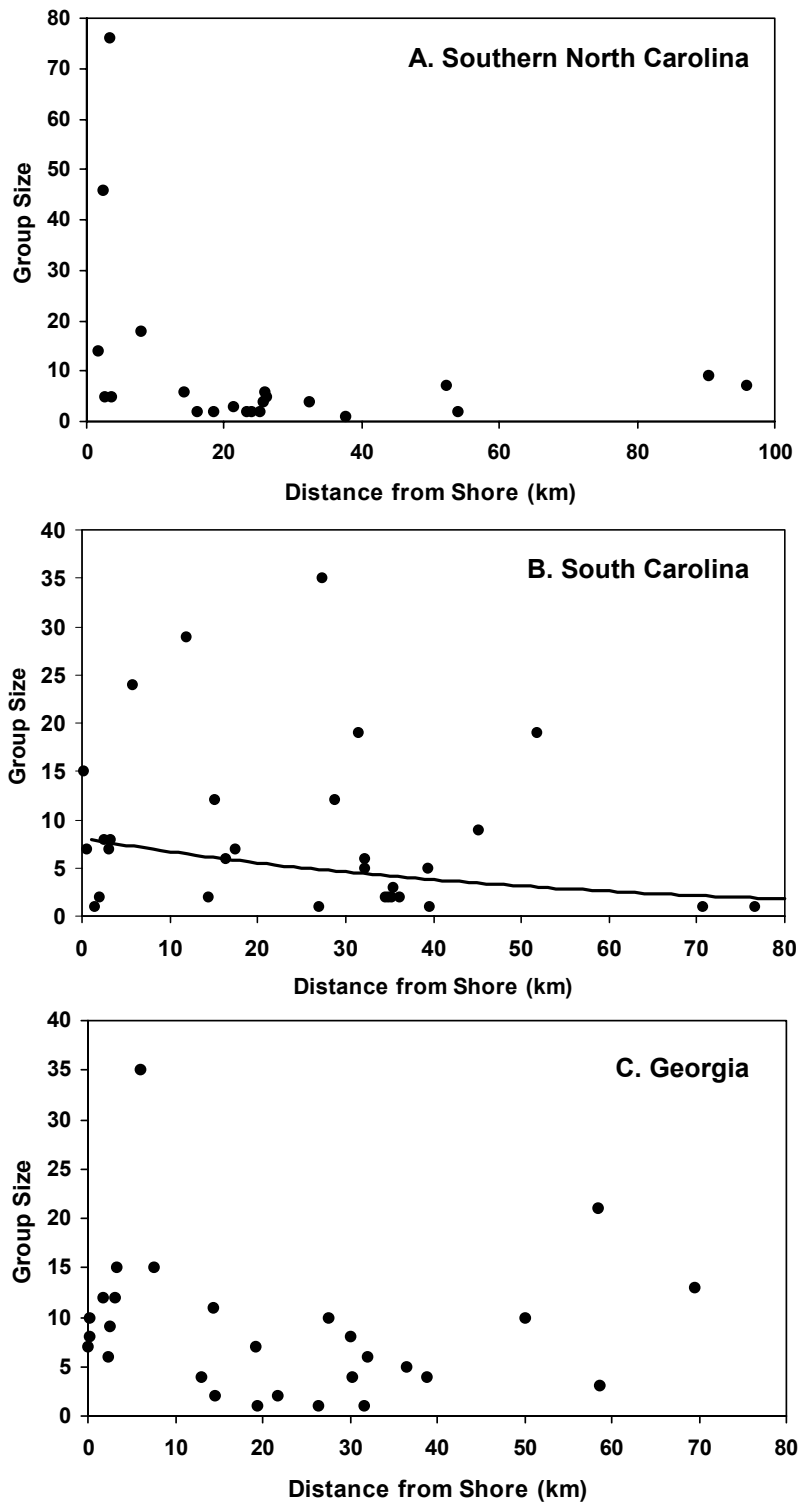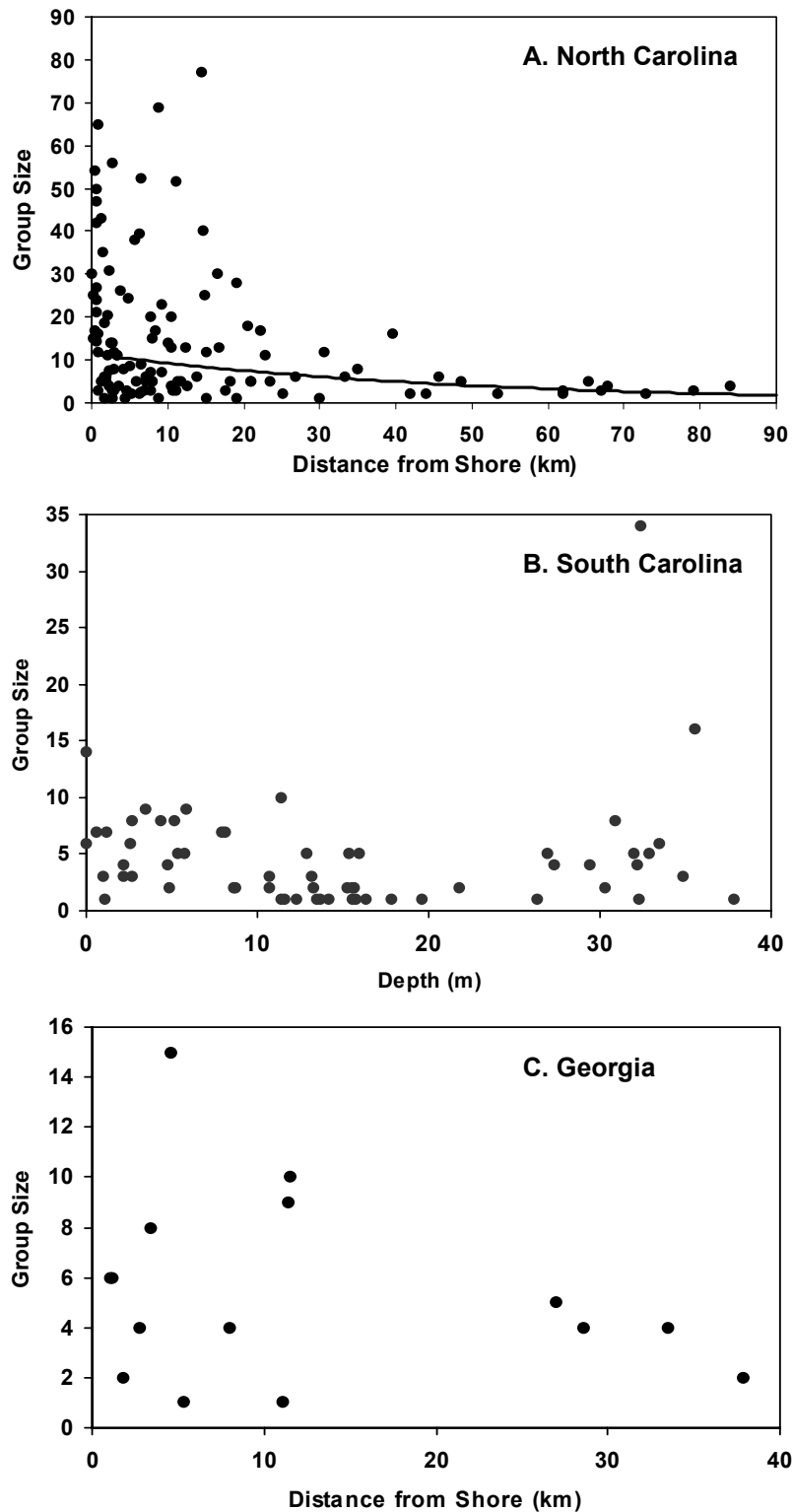
Figure 14. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer South Carolina management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
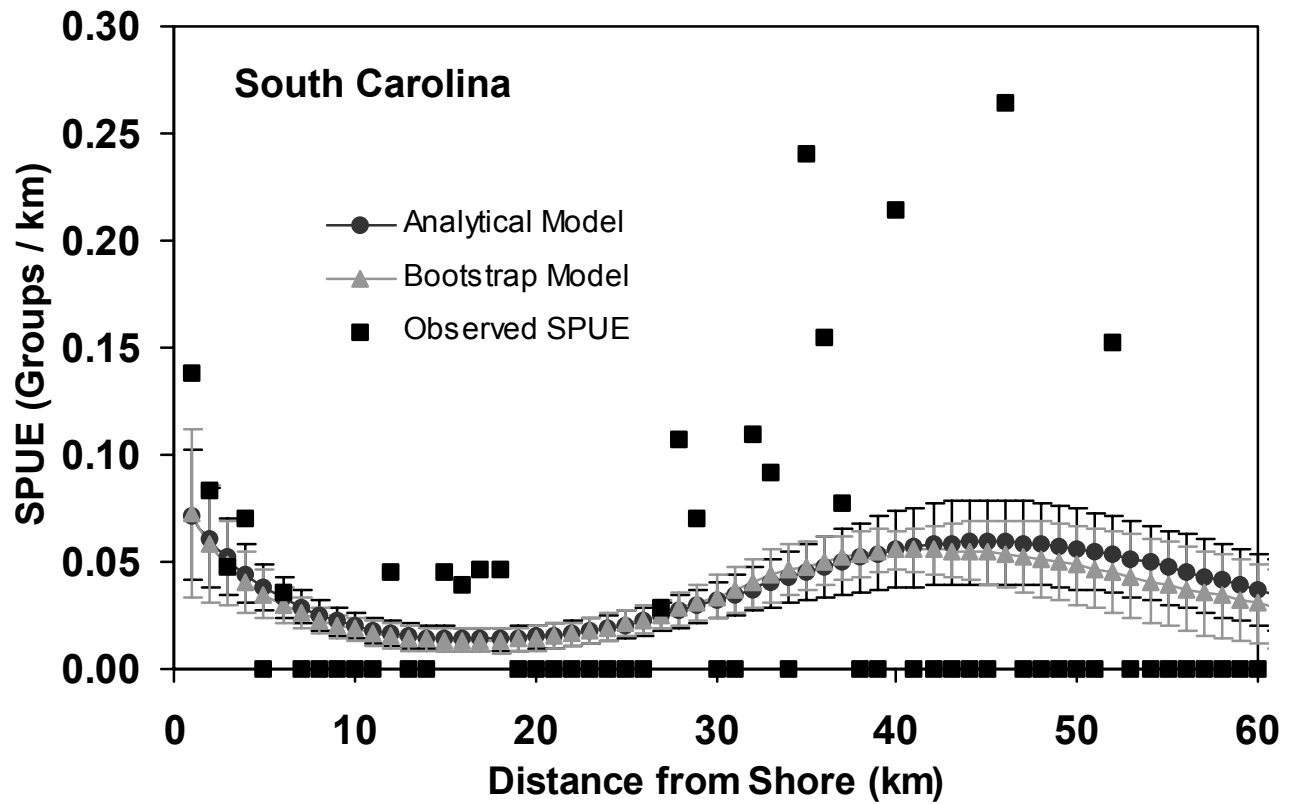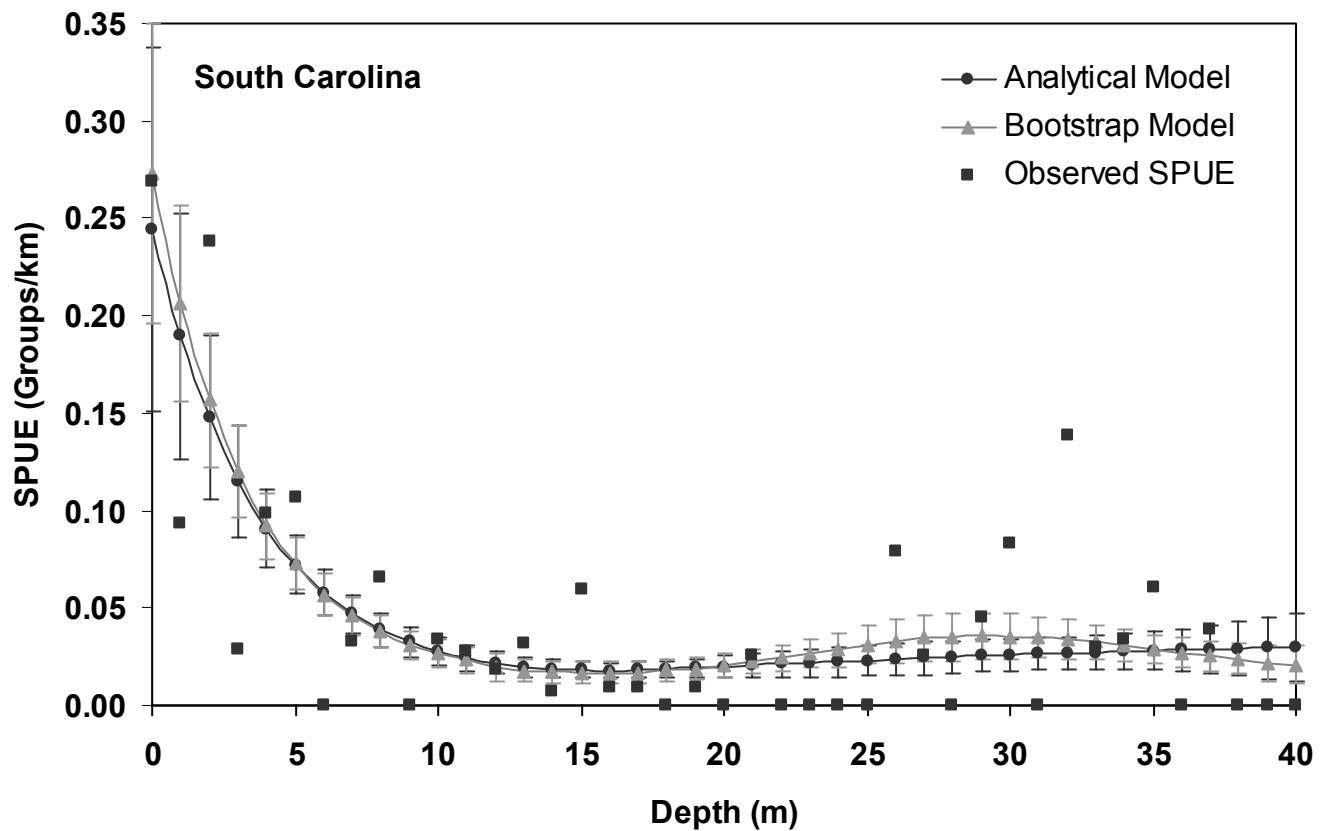
Figure 15. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer Georgia management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
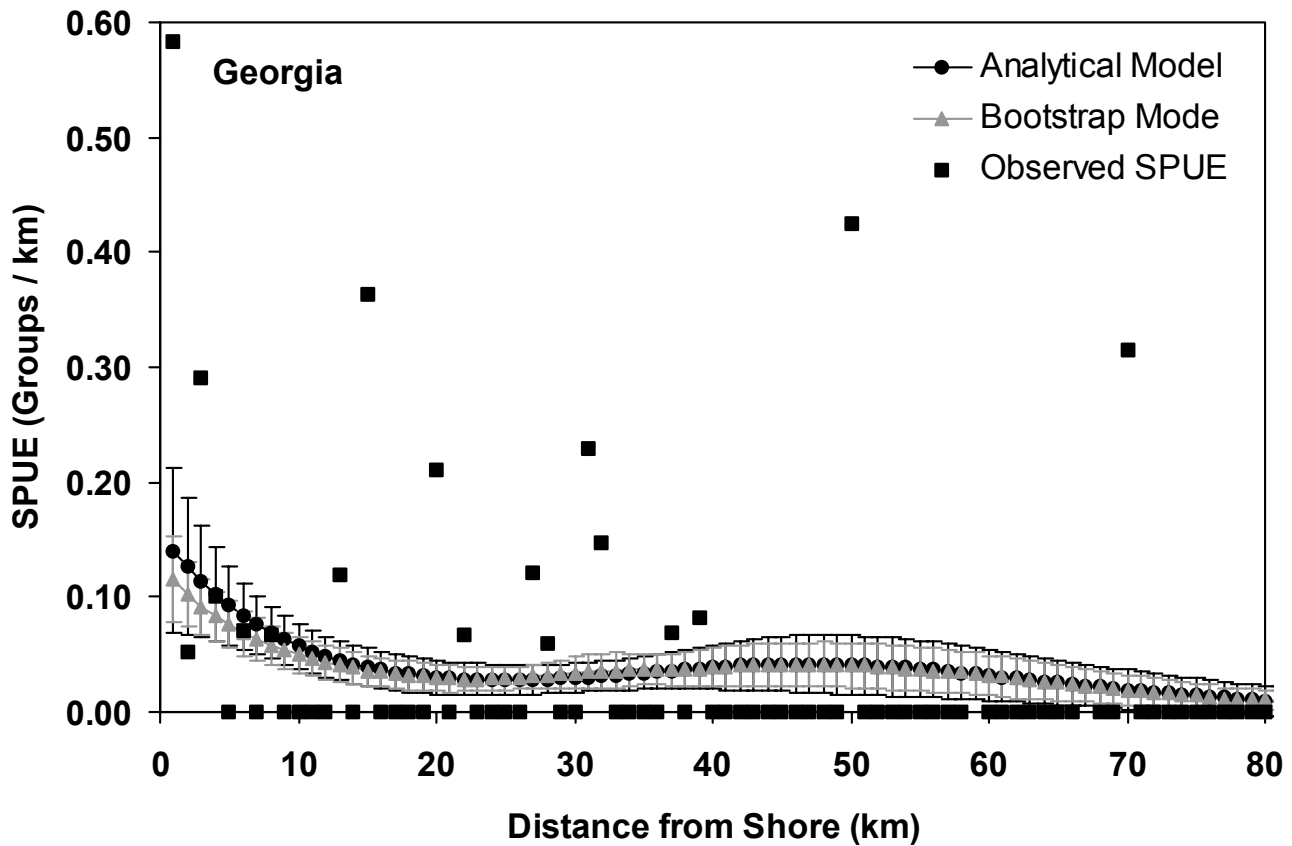
Figure 16. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer northern Florida management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
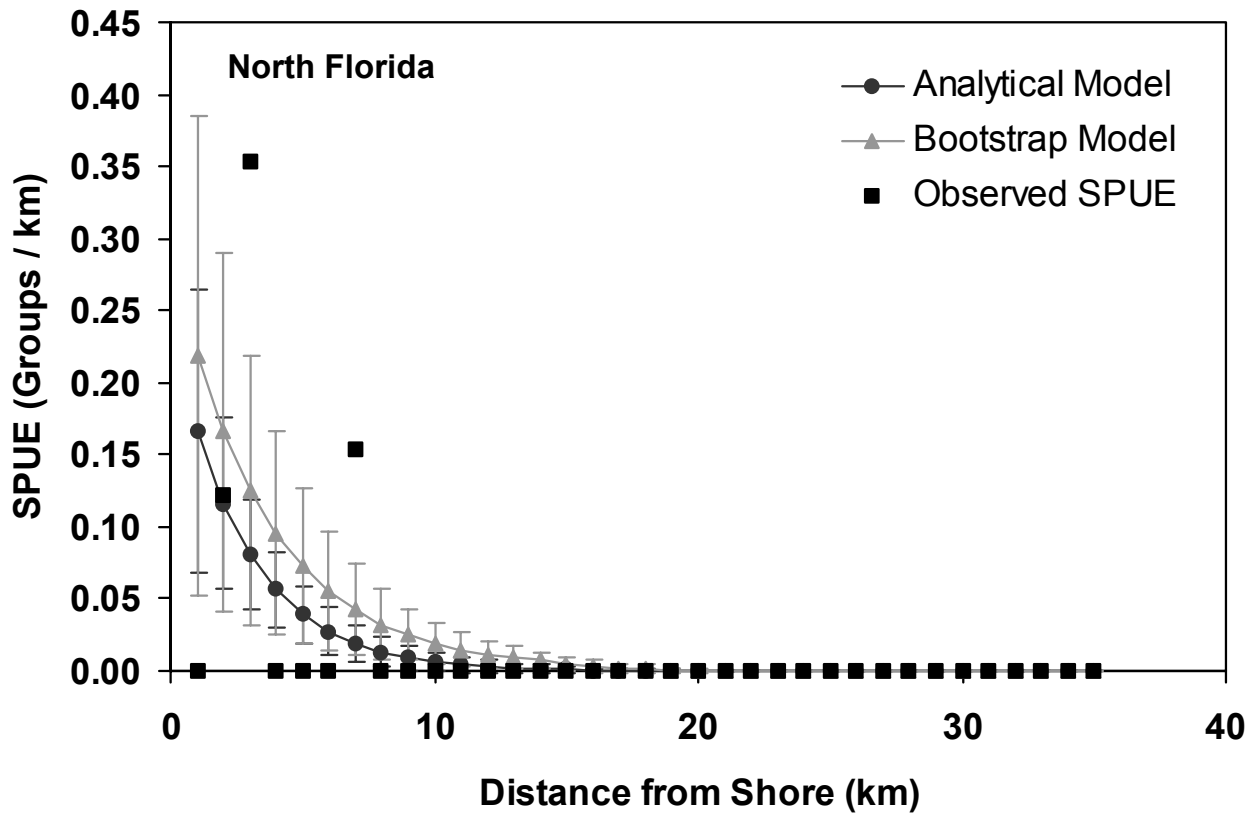
Figure 17. Number of animals per bottlenose dolphin groups during summer as a function of (A) distance from shore in the northern Florida unit and (B) depth in the central Florida unit.
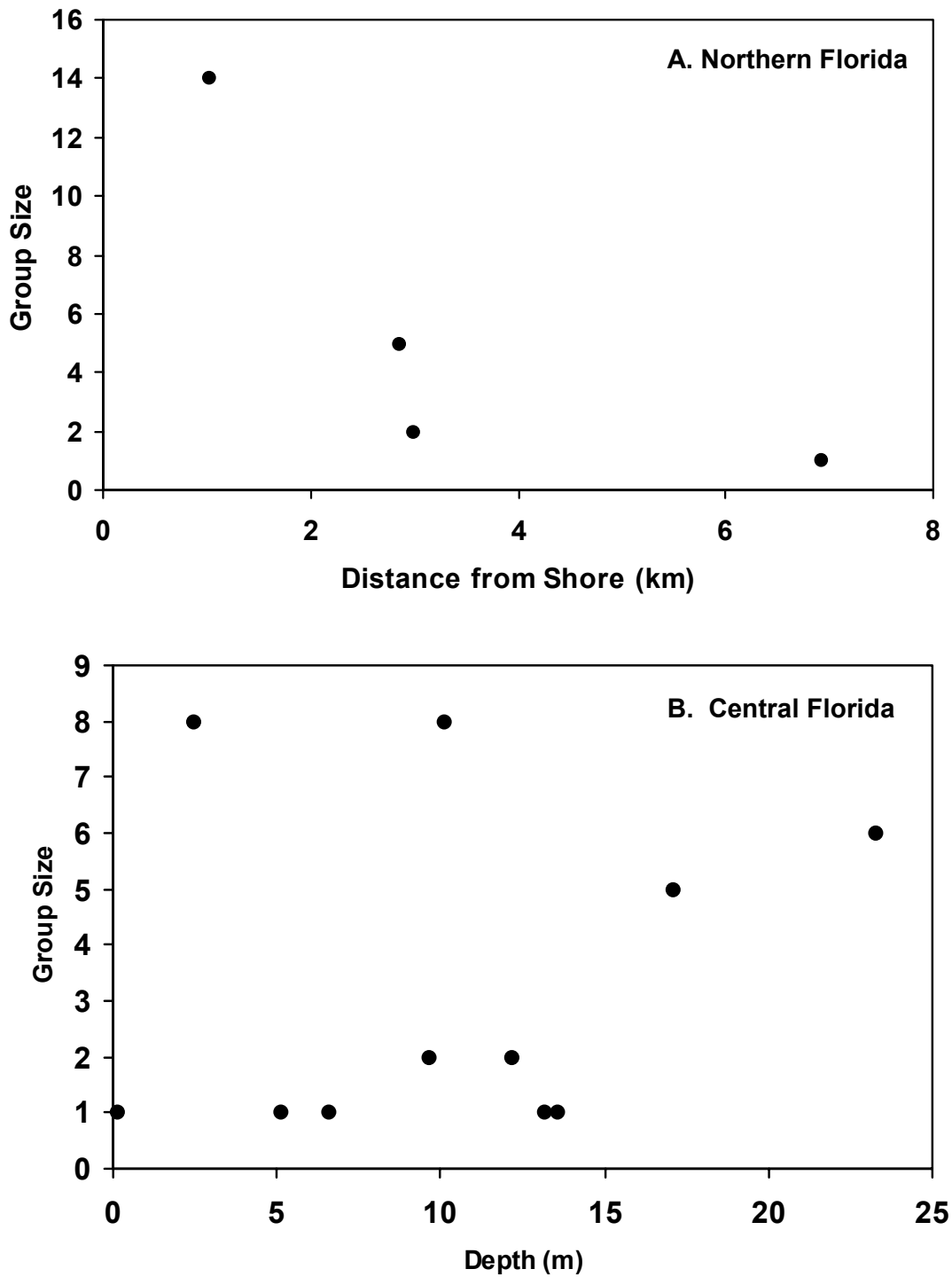
Figure 18. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the summer central Florida management unit. Observed SPUE values are summarized in 1 m depth intervals. Error bars indicate standard error of predicted values.
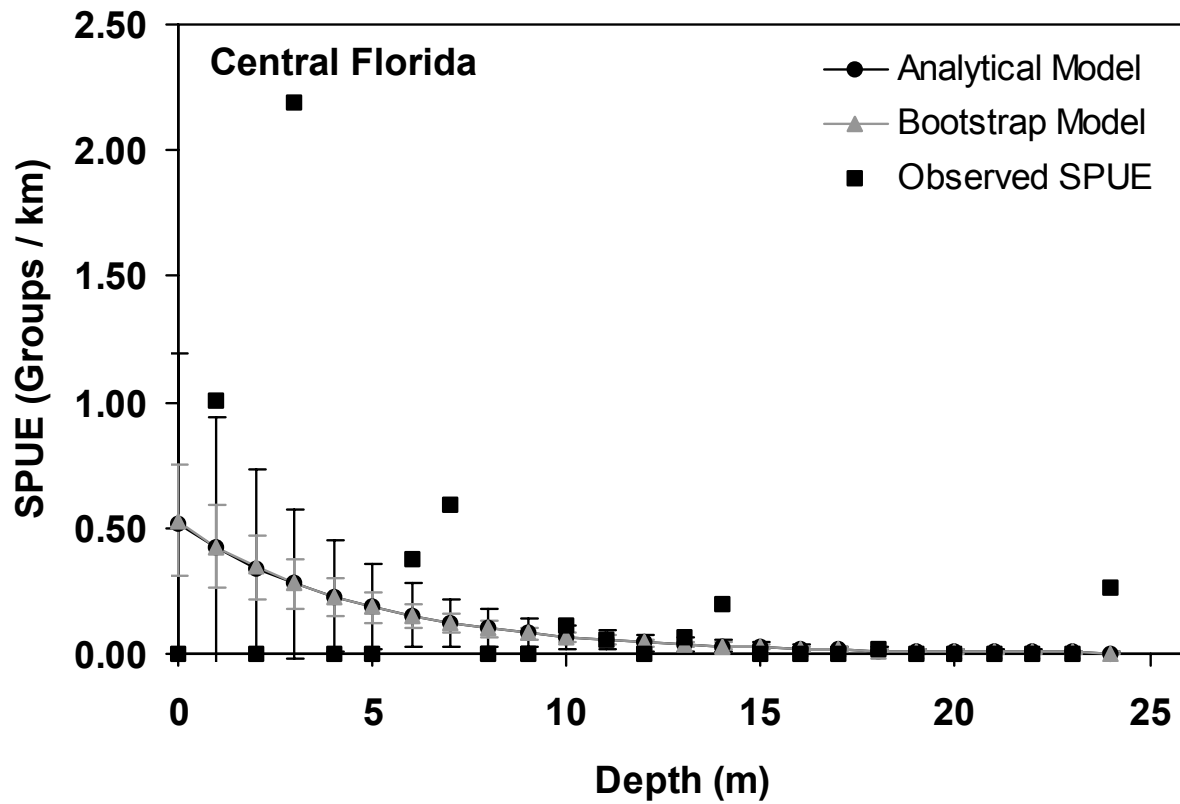
Figure 19. Observed dolphin group sightings per km of survey effort in 0.5 °C temperature bins in the North Carolina winter management units.
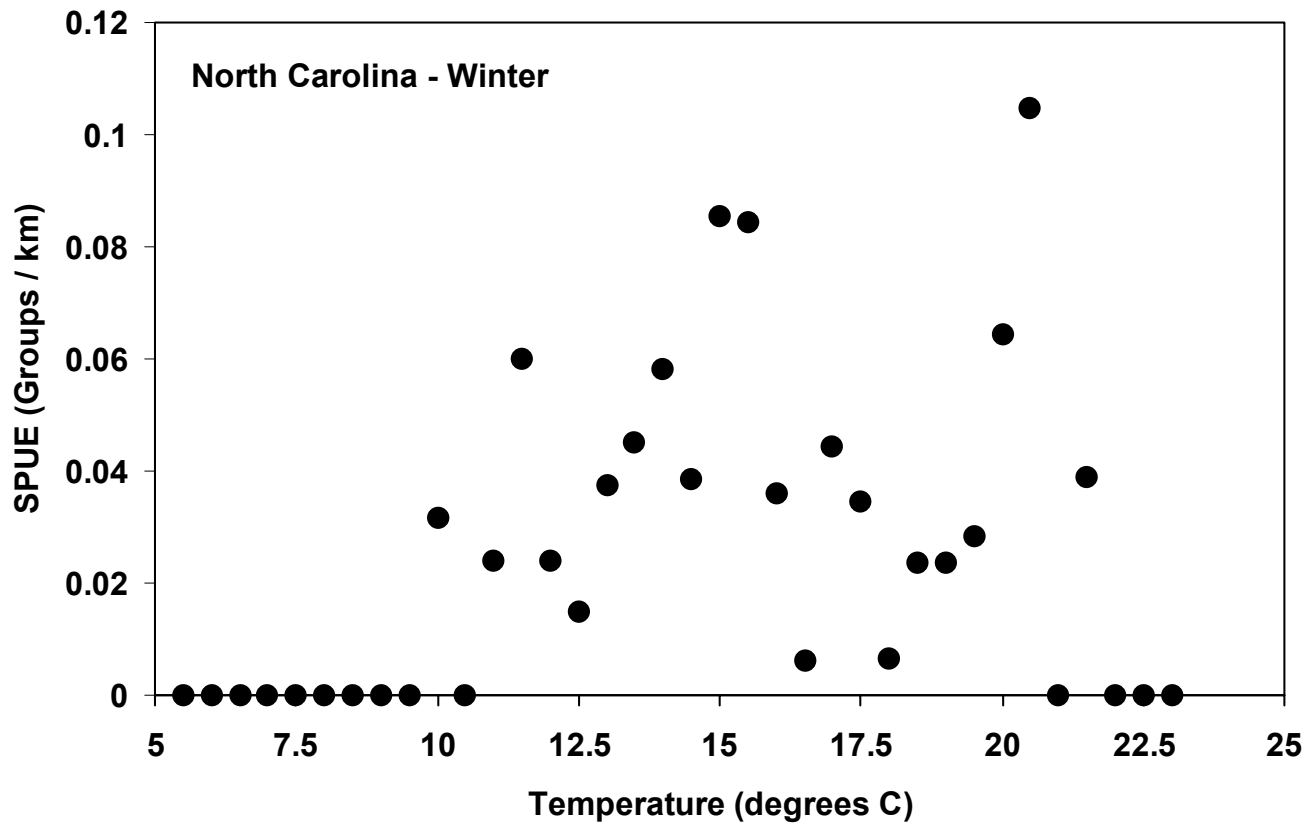
Figure 20. Distribution of bottlenose dolphin sightings north of Cape Hatteras, NC during winter 2002 aerial survey. Sea surface temperature (°C) is shown from an AHVRR image on 26 January 2002. Survey transects (dotted lines) and bottlenose dolphin groups (gray circles) are shown.

Figure 21. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the winter North Carolina management units. Fitted models and observed values for temperatures > 9.5 °C are shown. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.

Figure 22. Number of animals per bottlenose dolphin groups during winter as a function of (A) distance from shore in the North Carolina management units, (B) depth in the South Carolina unit, and (C) distance from shore in the Georgia unit. The fitted curve from a significant linear regression of distance from shore against log(Group Size) is shown (A).

Figure 23. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the winter South Carolina management unit. Observed SPUE values are summarized in 1 m depth intervals. Error bars indicate standard error of predicted values.

Figure 24. Dolphin groups sighted per km of trackline survey effort using the analytical and bootstrapped GAM models for the winter Georgia management unit. Observed SPUE values are summarized in 1 km distance from shore intervals. Error bars indicate standard error of predicted values.
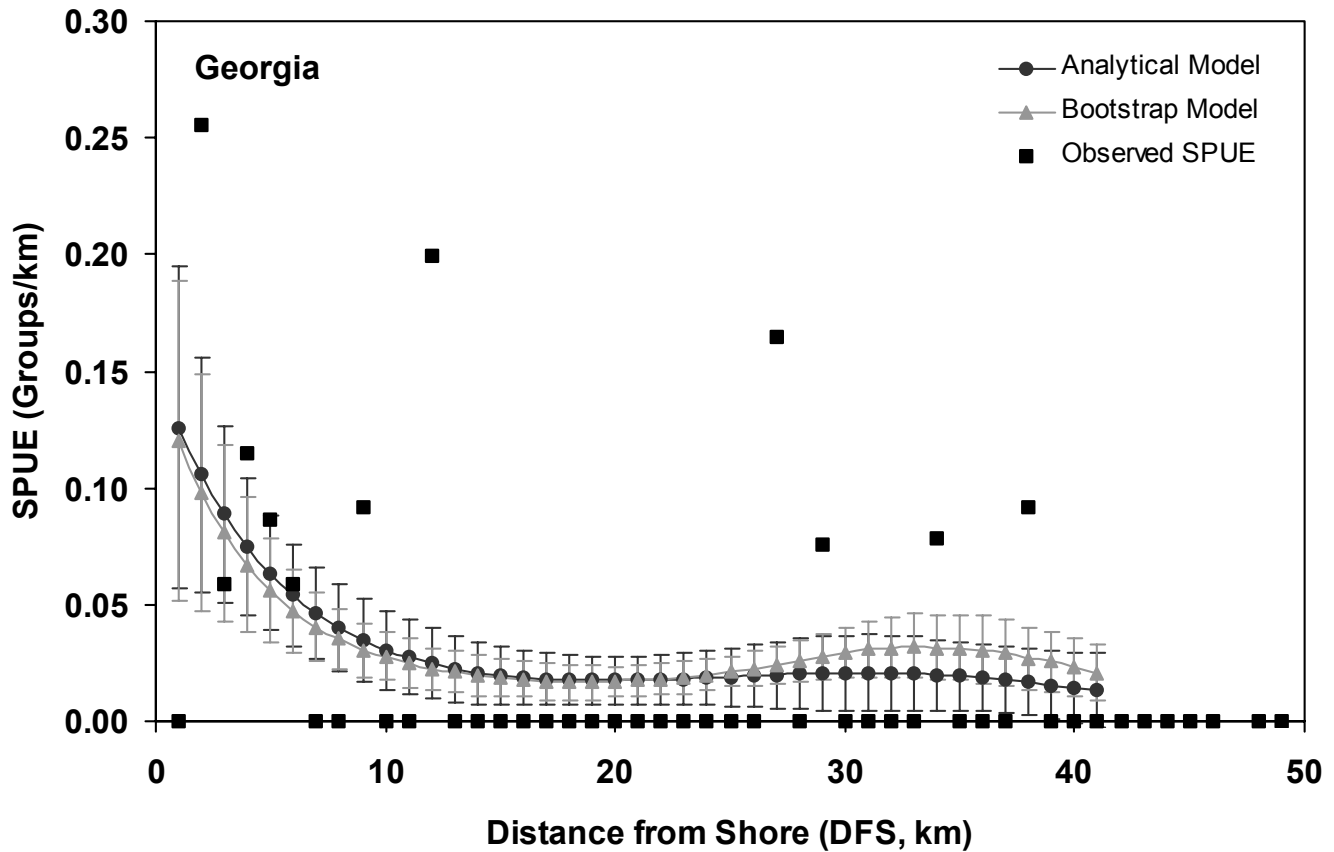
Figure 25. Biopsy sample locations and identification from large and small vessel surveys during summer 1998-2002.
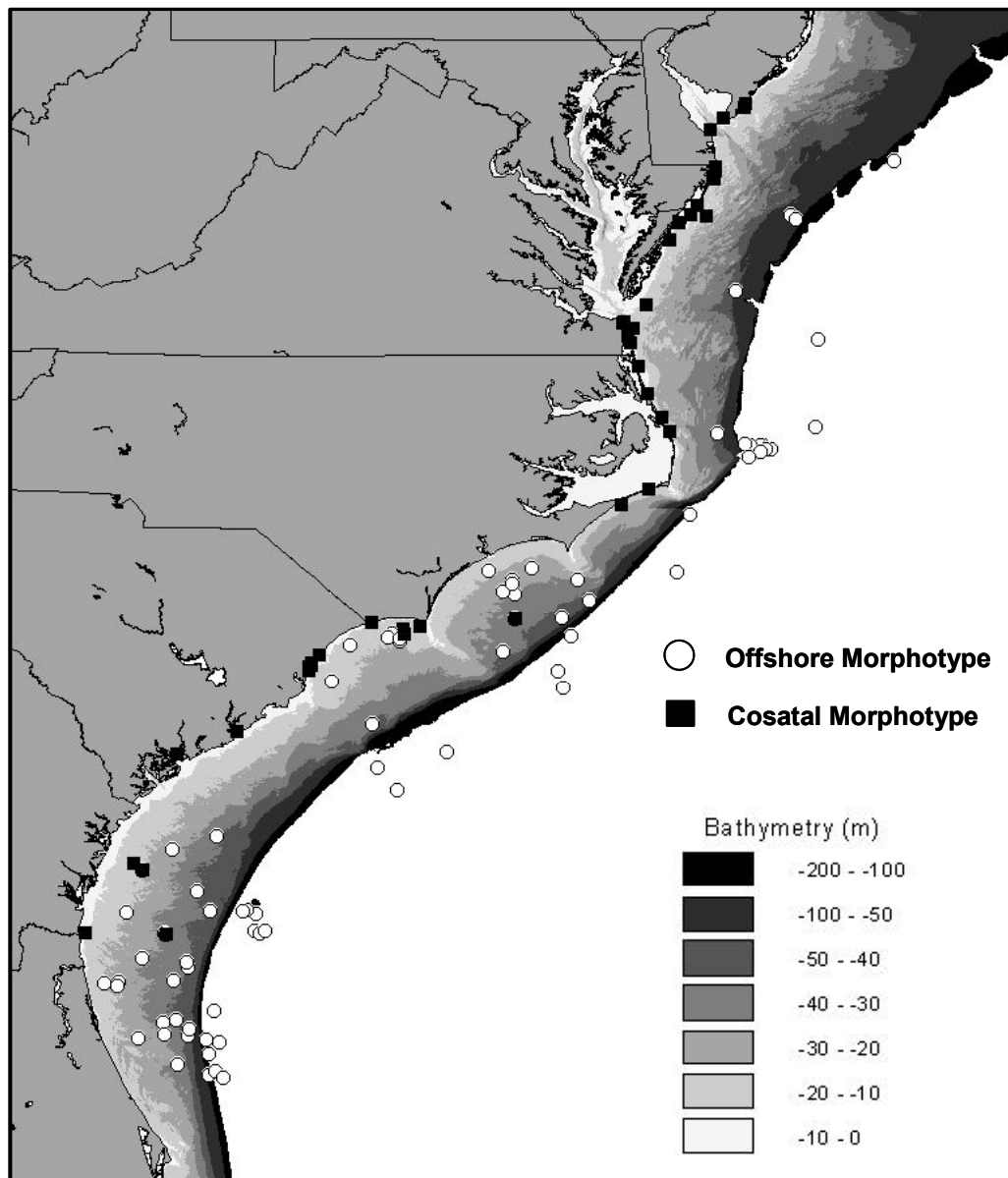
Figure 26. Biopsy sample locations and identification from a large vessel survey and local sampling efforts during winter 2002.
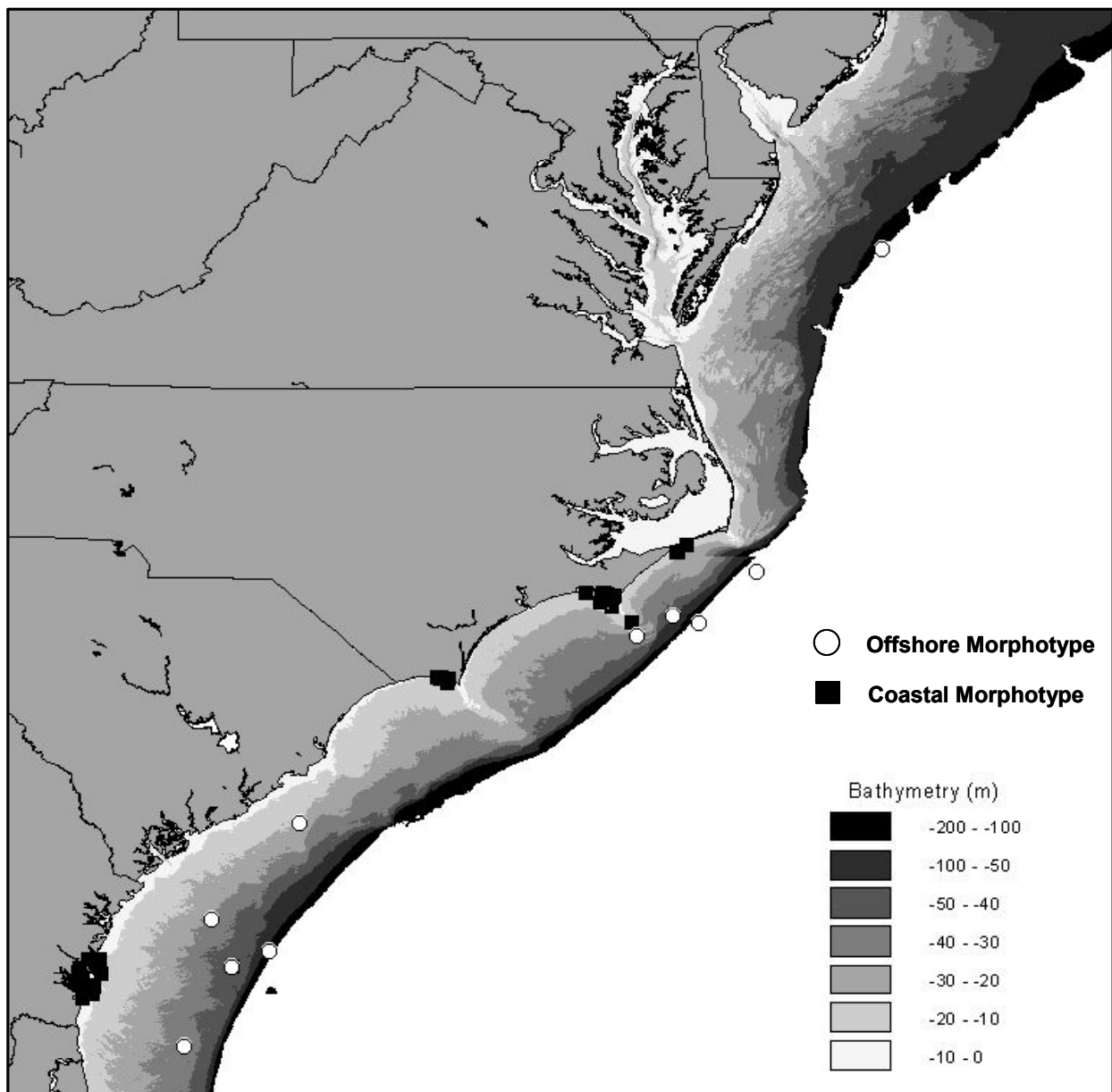
Figure 27. Distribution of biopsy sample locations in the northern migratory and northern North Carolina management units during summer with respect to (A) depth and (B) distance from shore.
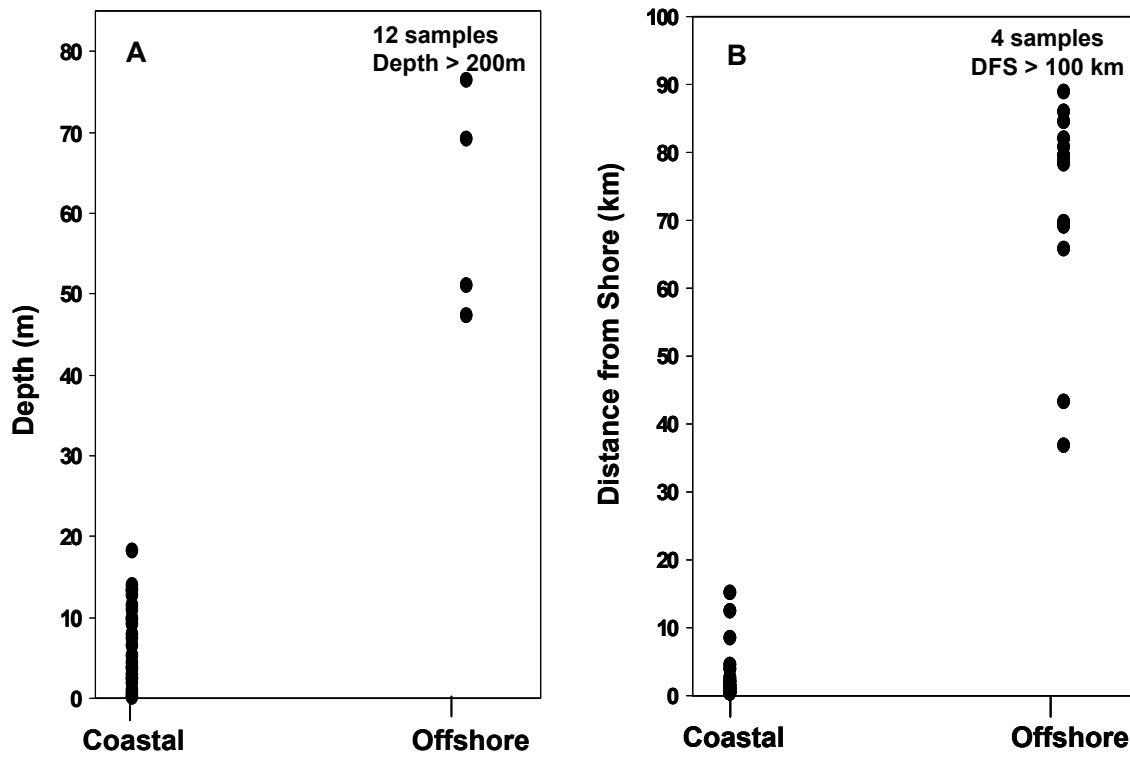
Figure 28. Logistic regression model for summer biopsies in management units south of Cape Lookout. Observed data values are shown (squares). Coastal morphotype samples have a value of 1 on the y-axis while offshore morphotypes = 0. Error bars indicate 95% confidence intervals for the logistic regression model.
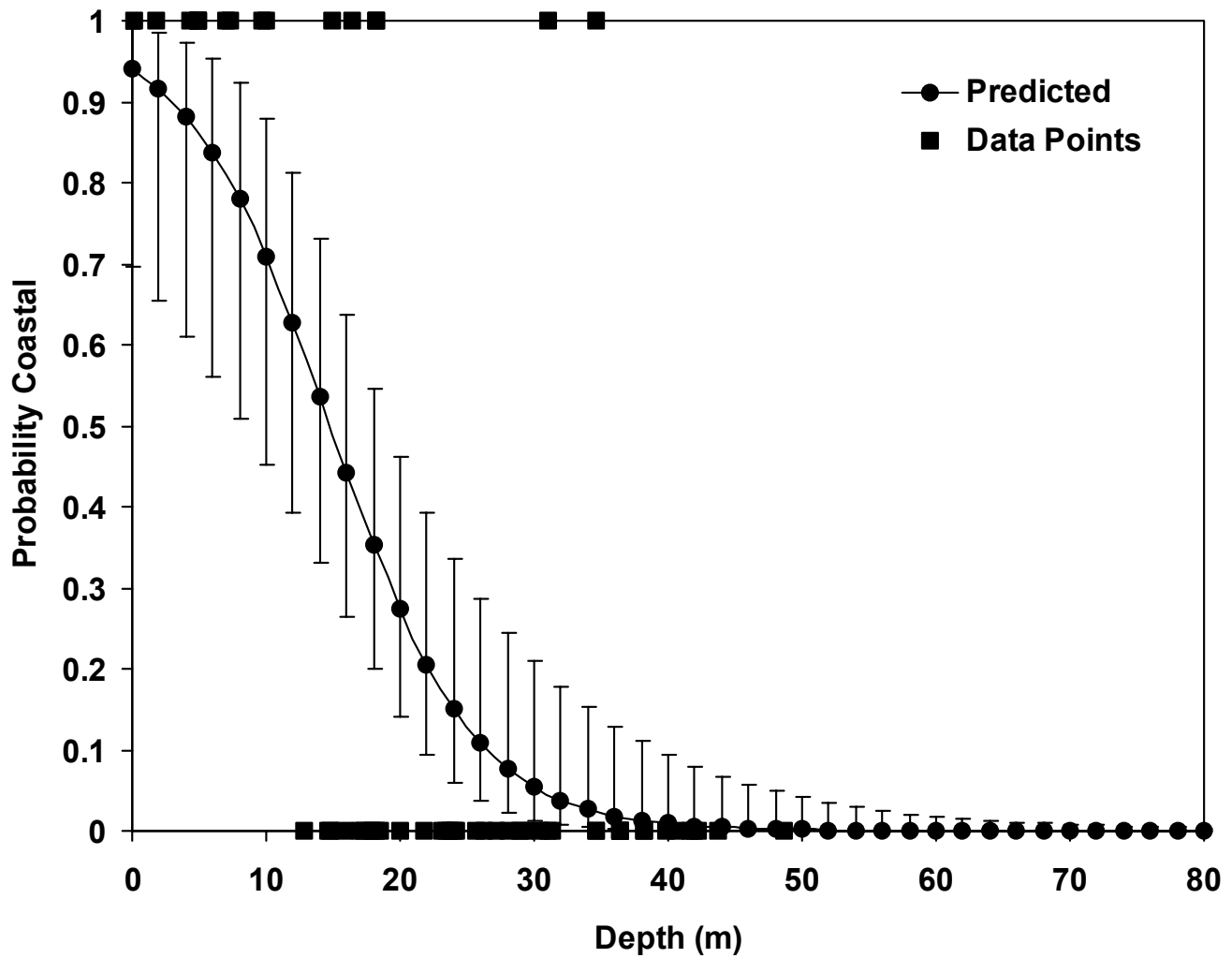
Figure 29. Logistic regression model for winter biopsies in the North Carolina management unit. Observed data values are shown (squares). Coastal morphotype samples have a value of 1 on the y-axis while offshore morphotypes = 0. Error bars indicate 95% confidence intervals for the logistic regression model.
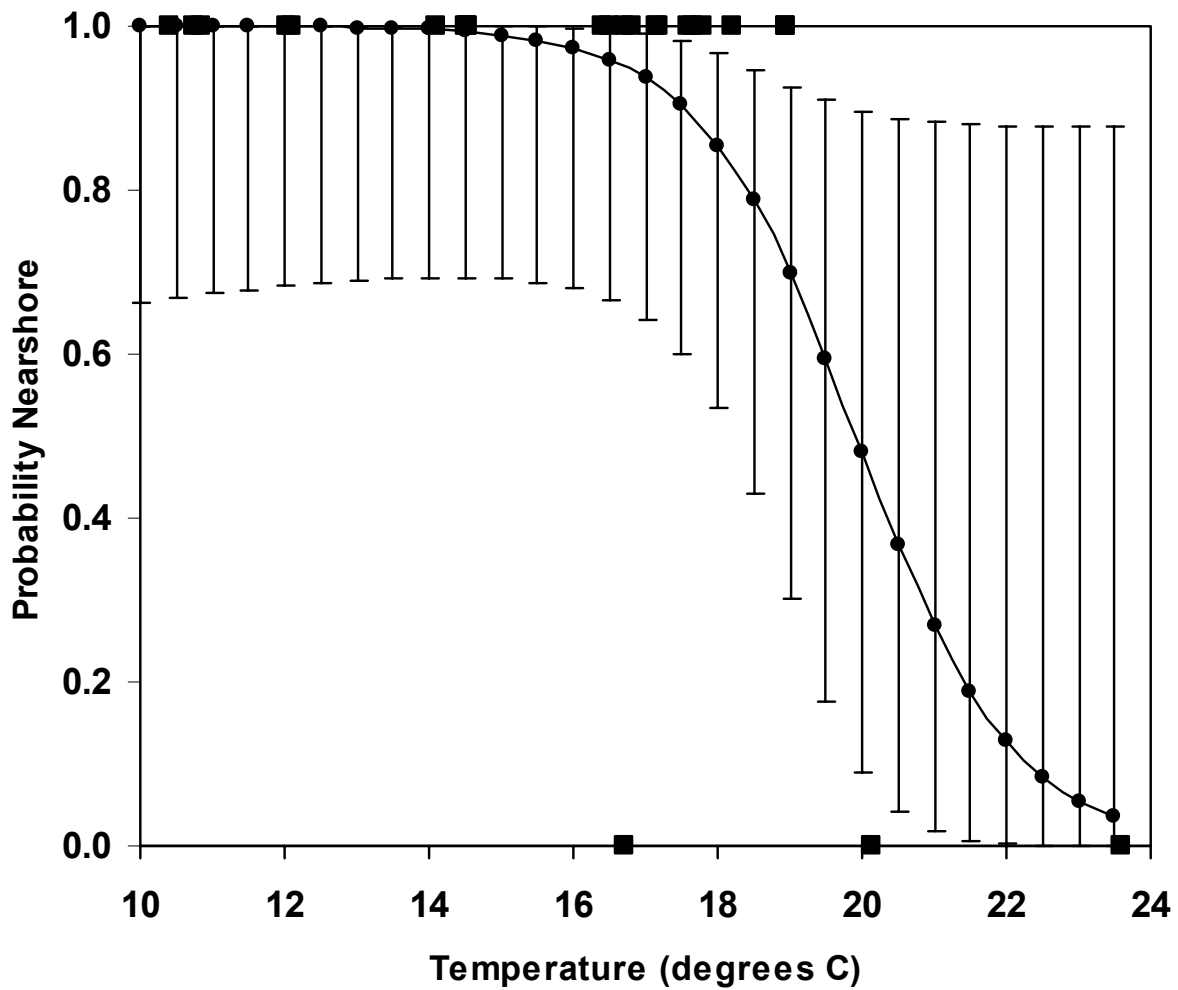
Figure 30. Logistic regression model for winter biopsies in the Georgia management unit. Observed data values are shown (squares). Coastal morphotype samples have a value of 1 on the y-axis while offshore morphotypes = 0. Error bars indicate 95% confidence intervals for the logistic regression model.
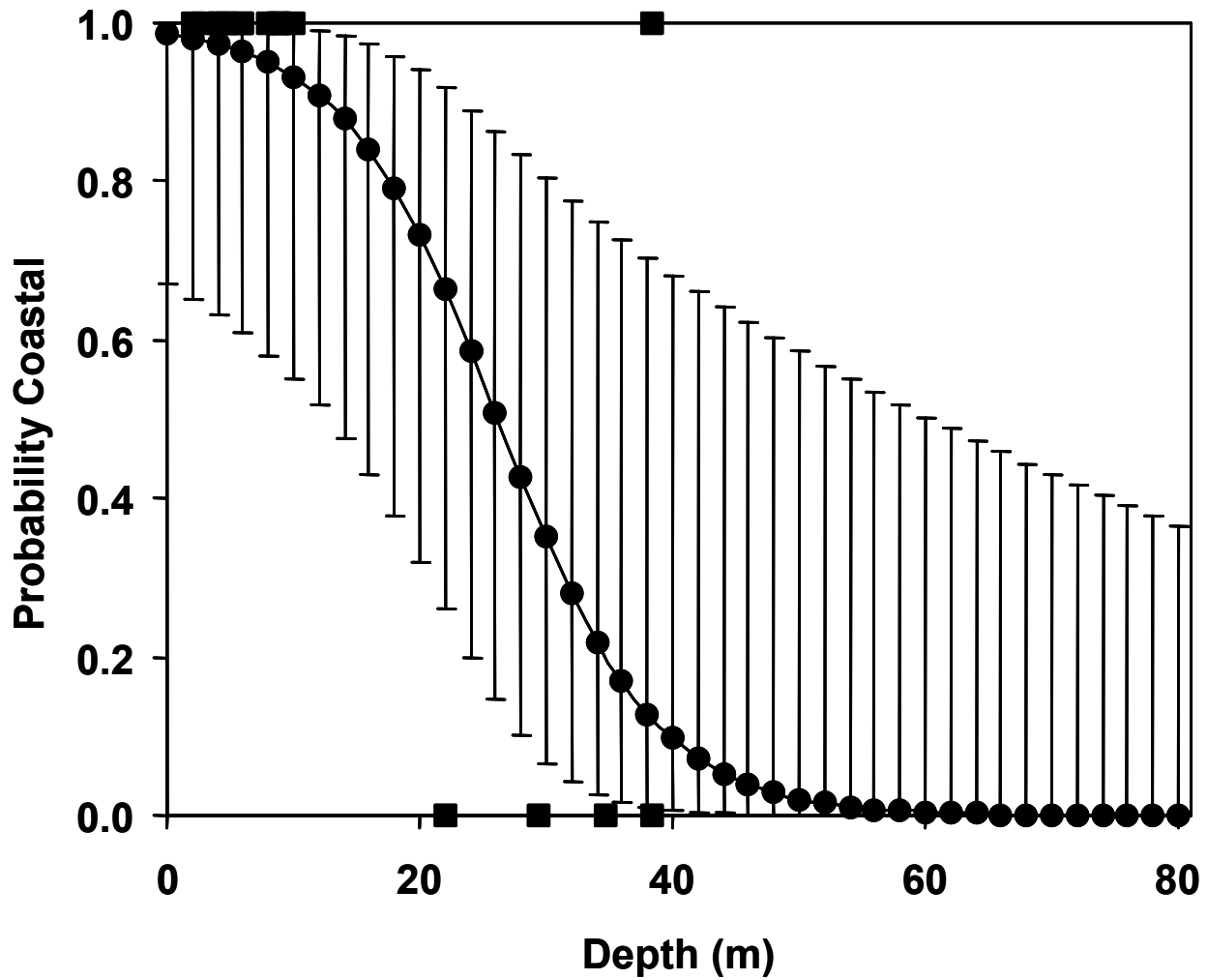
Figure 31. Sighting probability as function of perpendicular sighting distance for summer 2002. Predicted function (line) is a smoothing spline fit to observed sighting frequencies. Observed sighting probabilities (points) in 50 m distance intervals are shown.
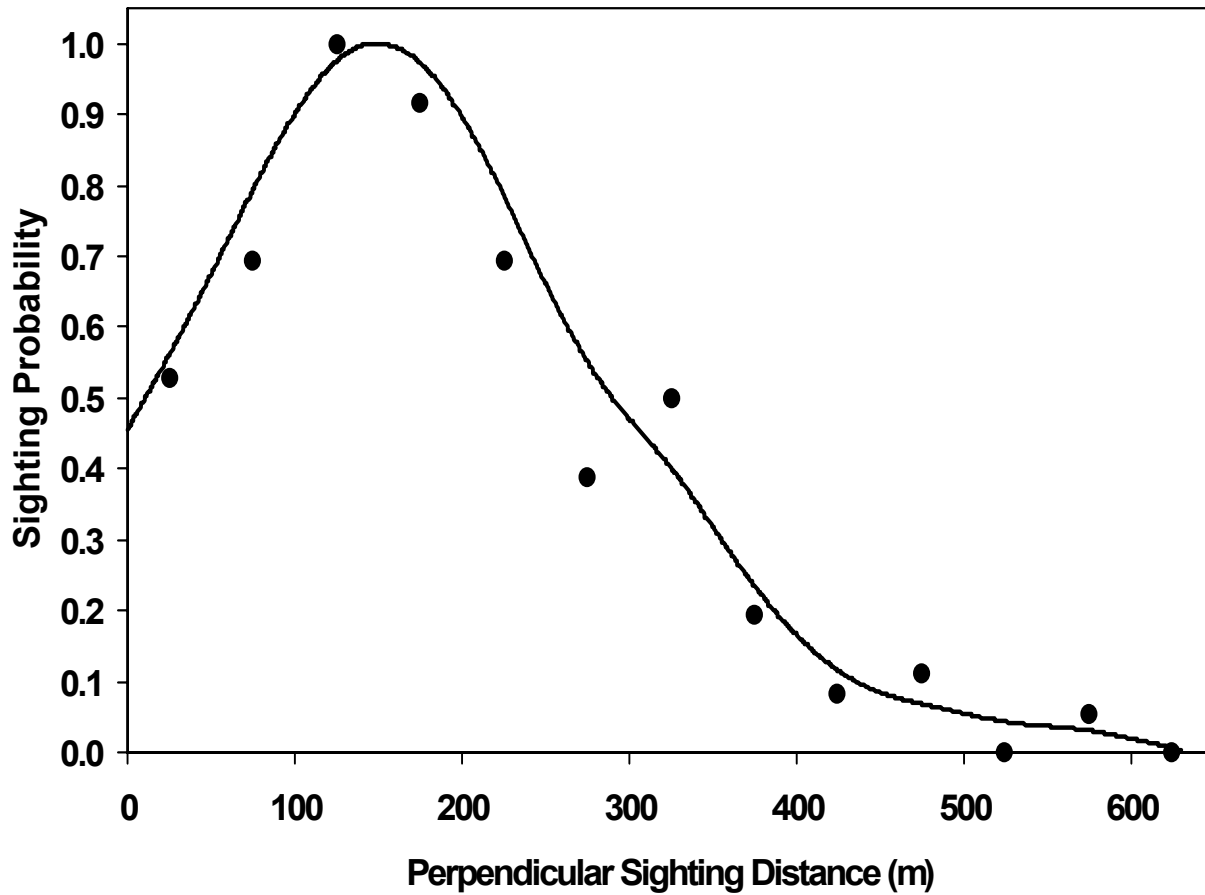
Figure 32. Sighting probability as function of perpendicular sighting distance for winter 2002. Predicted function (line) is a smoothing spline fit to observed sighting frequencies. Observed sighting probabilities (points) in 50 m distance intervals are shown.
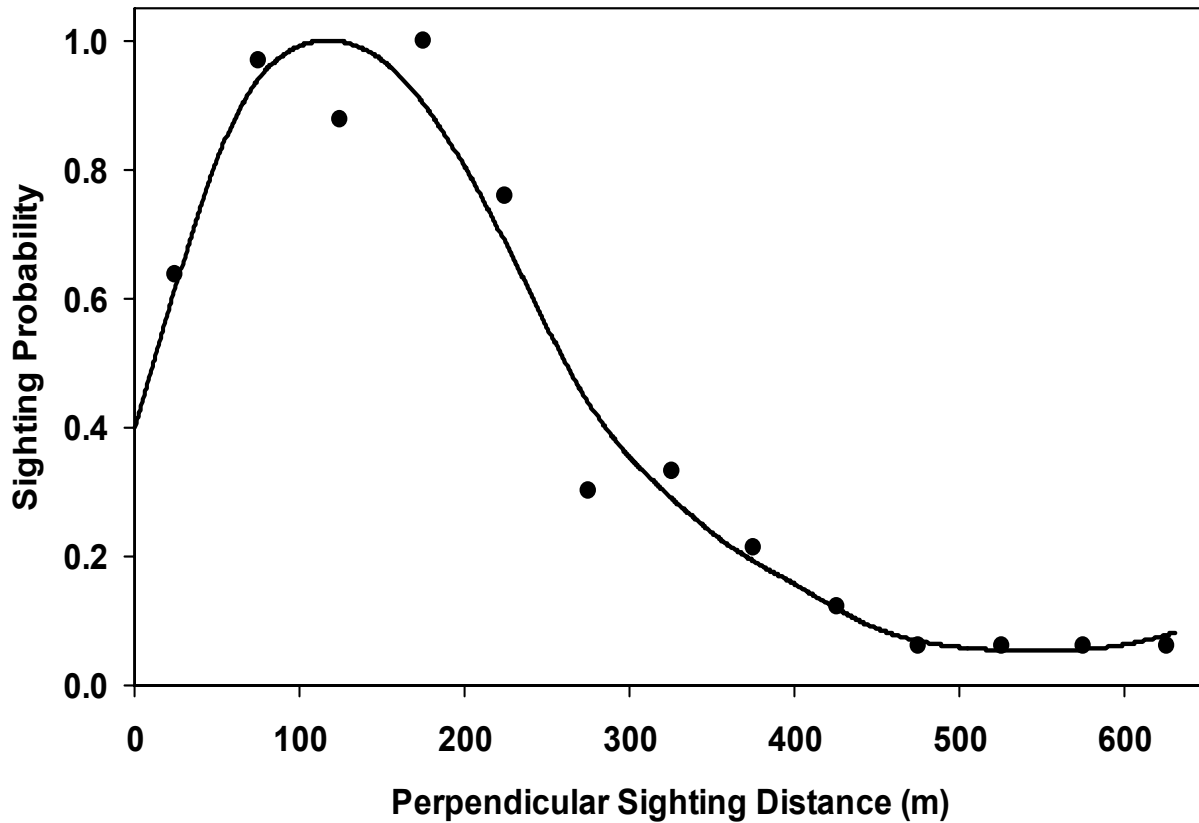
Figure 33. Number of animals observed during summer aerial surveys by depth interval in the southern North Carolina, South Carolina, Georgia, northern Florida, and central Florida management units. The predicted proportion of coastal morphotype animals and 95% confidence interval for the logistic regression model is shown.
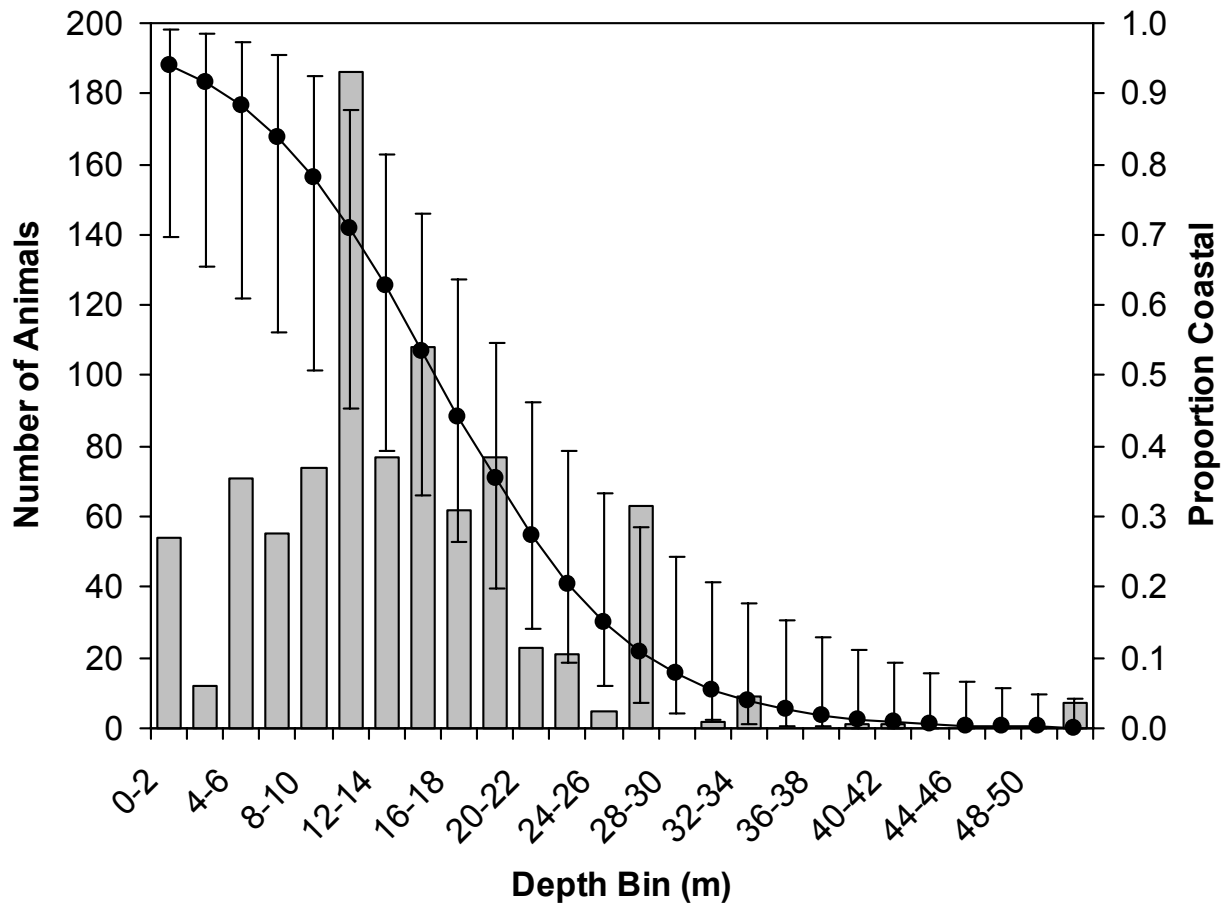
Figure 34. Number of animals observed during the winter 2002 survey and predicted proportion coastal from the logistic regression model by (A) Temperature interval for the North Carolina management unit and (B) depth interval for the South Carolina and Georgia management units. Error bars indicate 95% confidence intervals of the logistic regression.
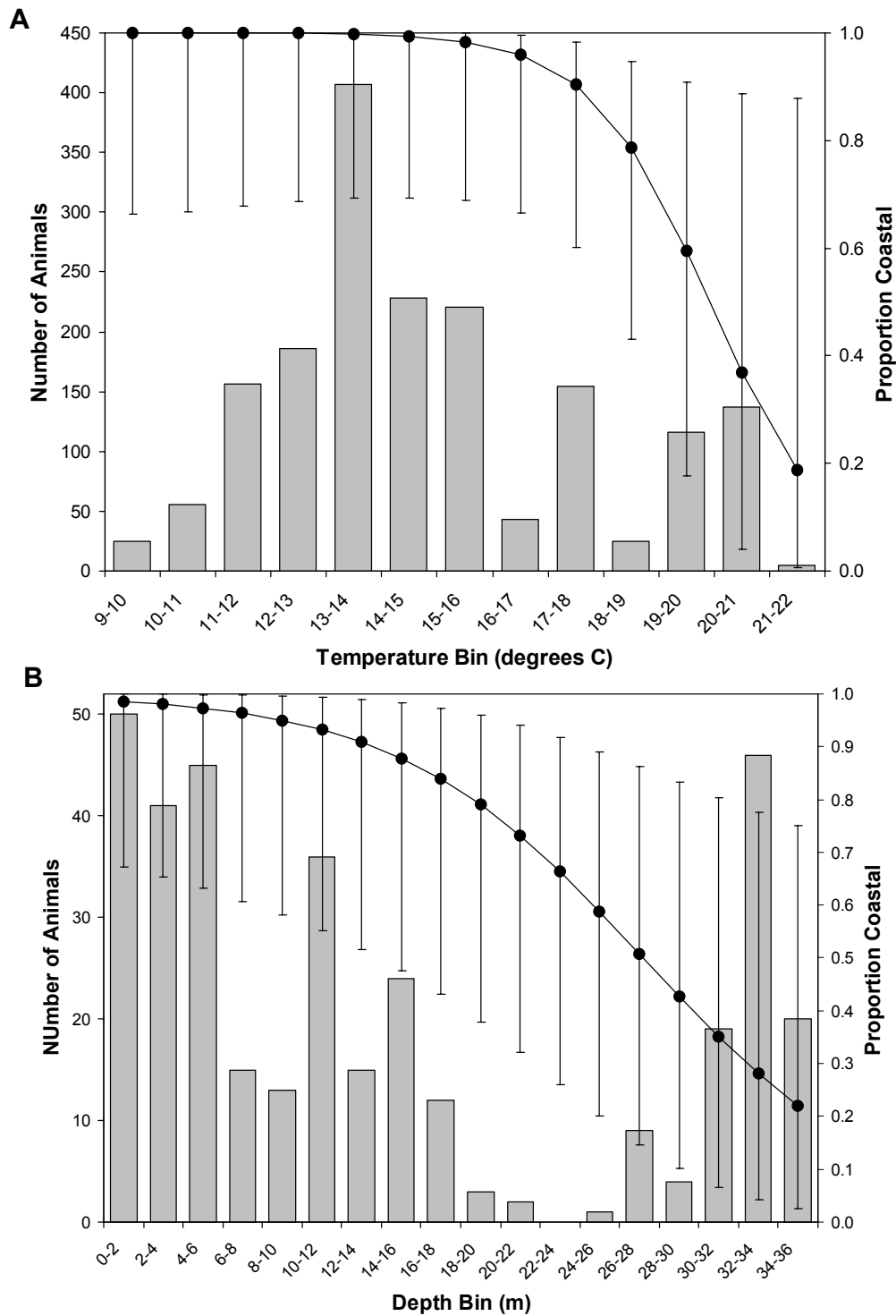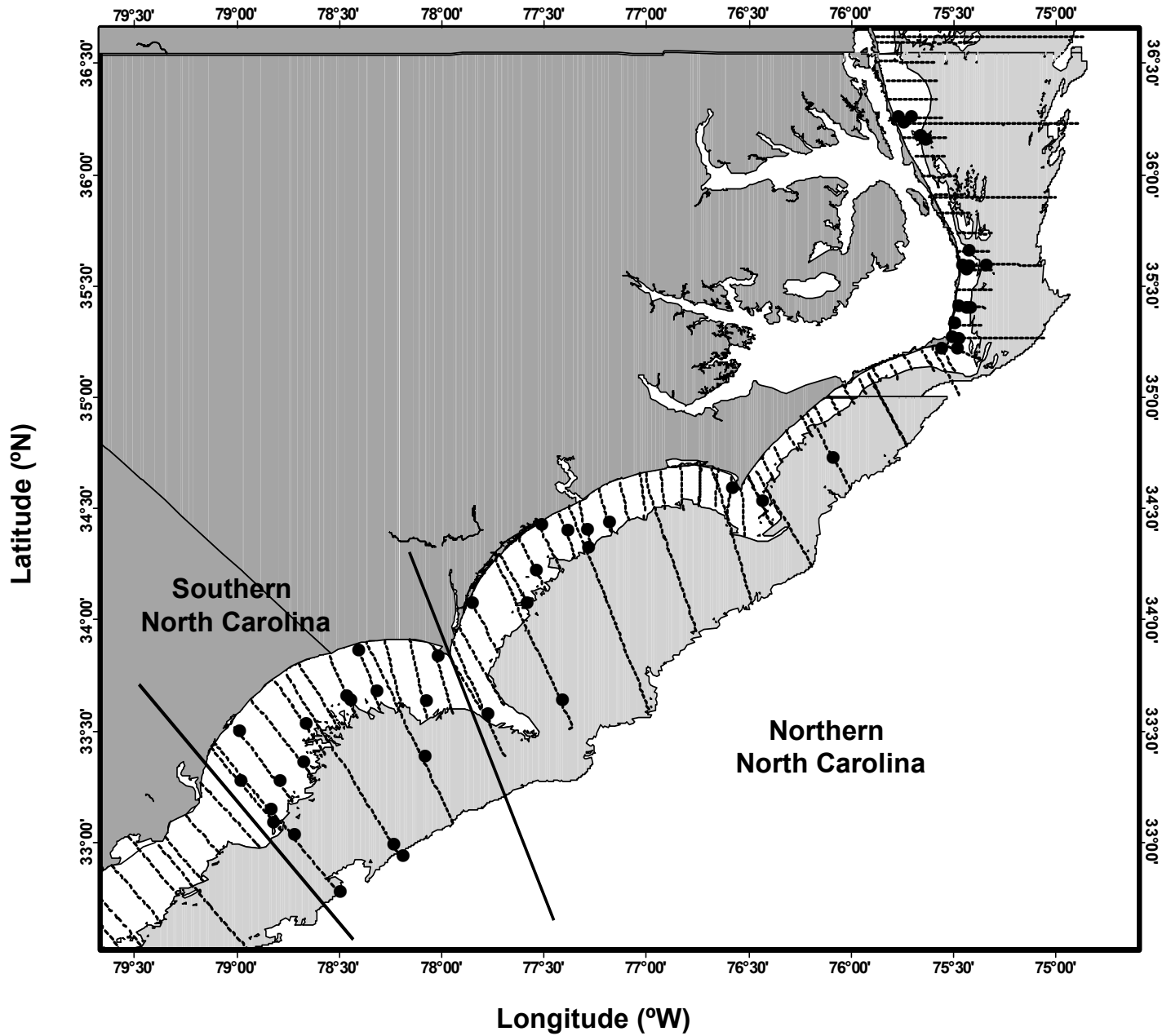
Appendix

Maps of bottlenose dolphin group locations for each management unit.
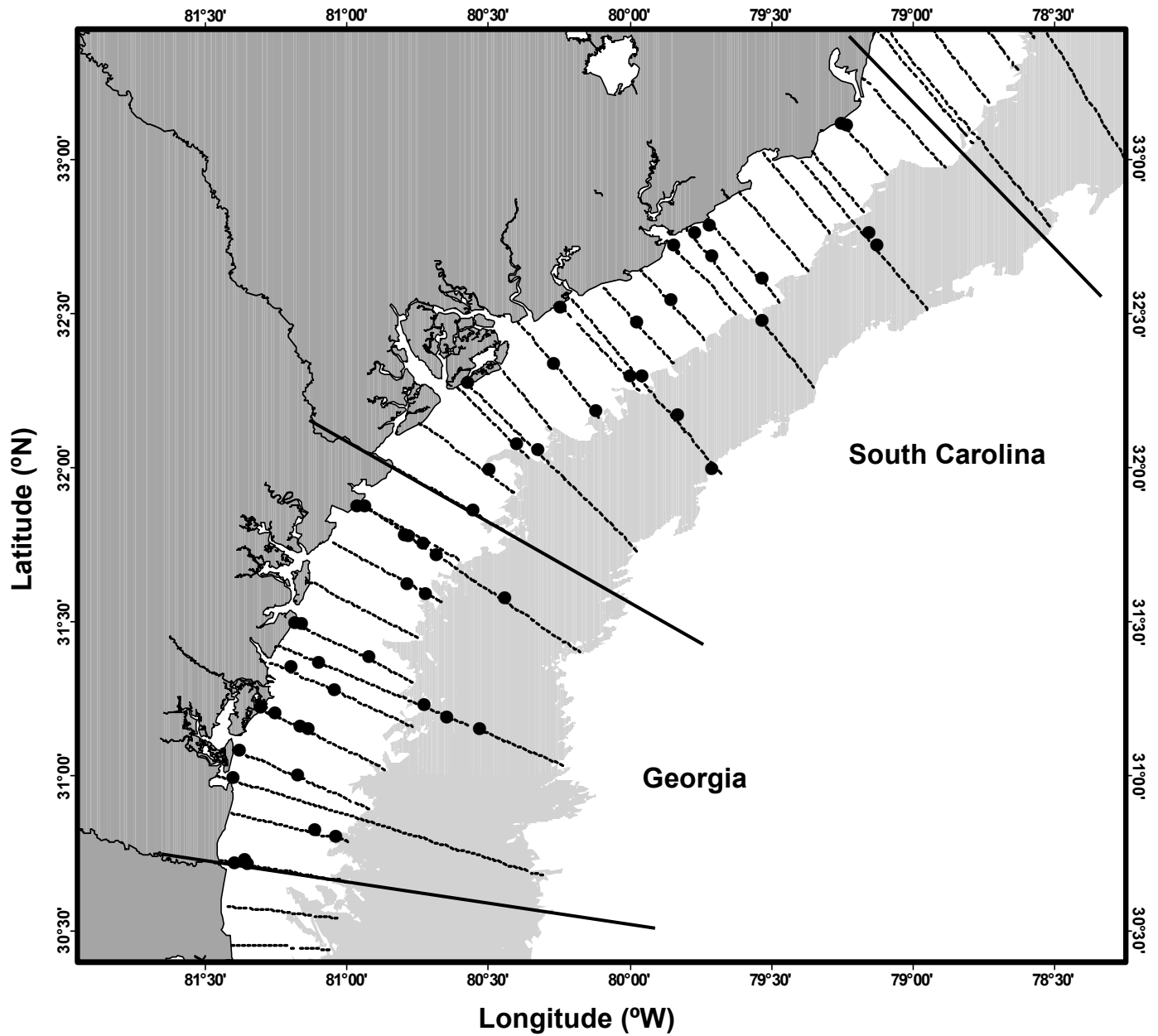
Appendix Fig. 1: Bottlenose dolphin sightings in the northern migratory unit during summer 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.
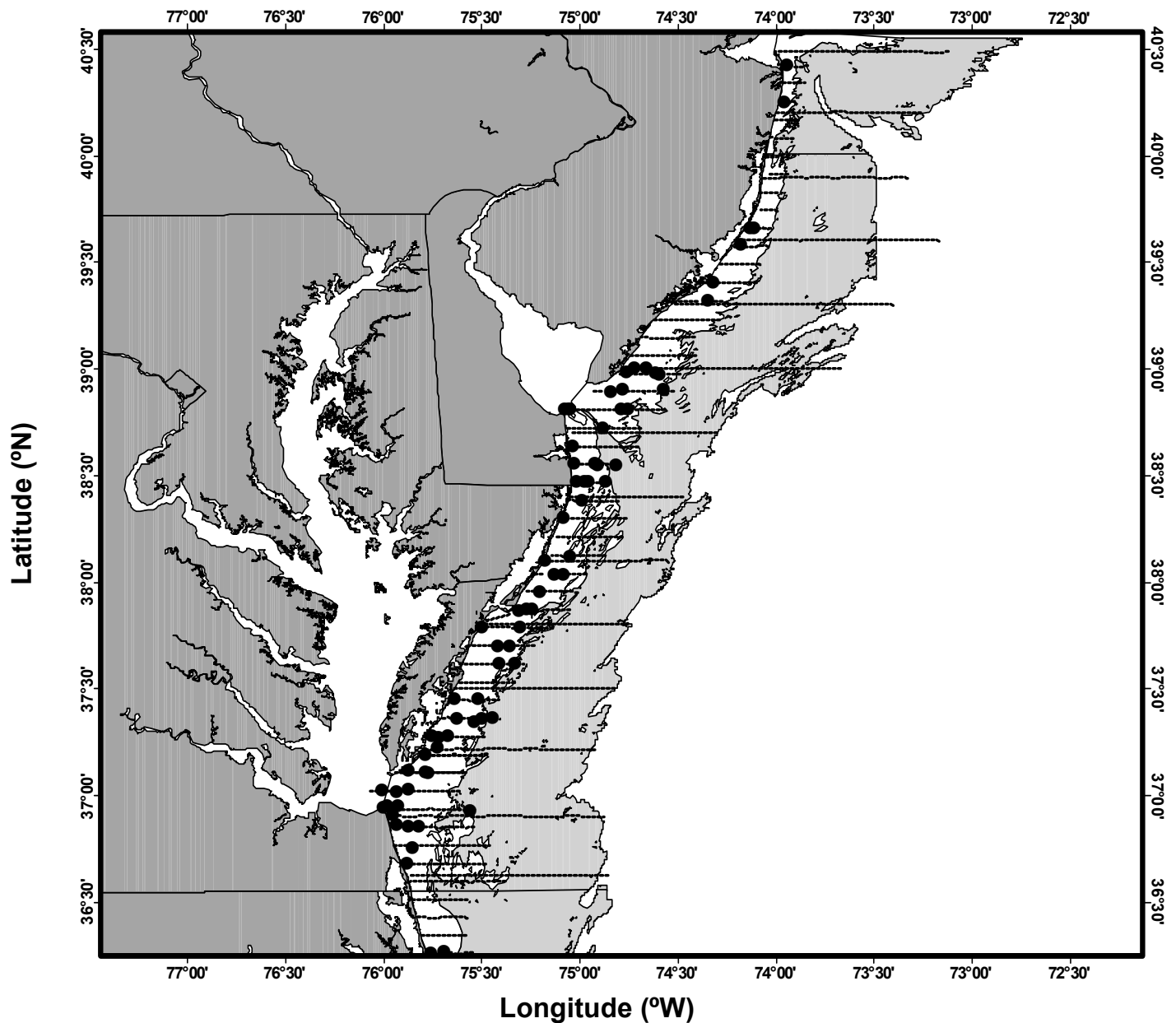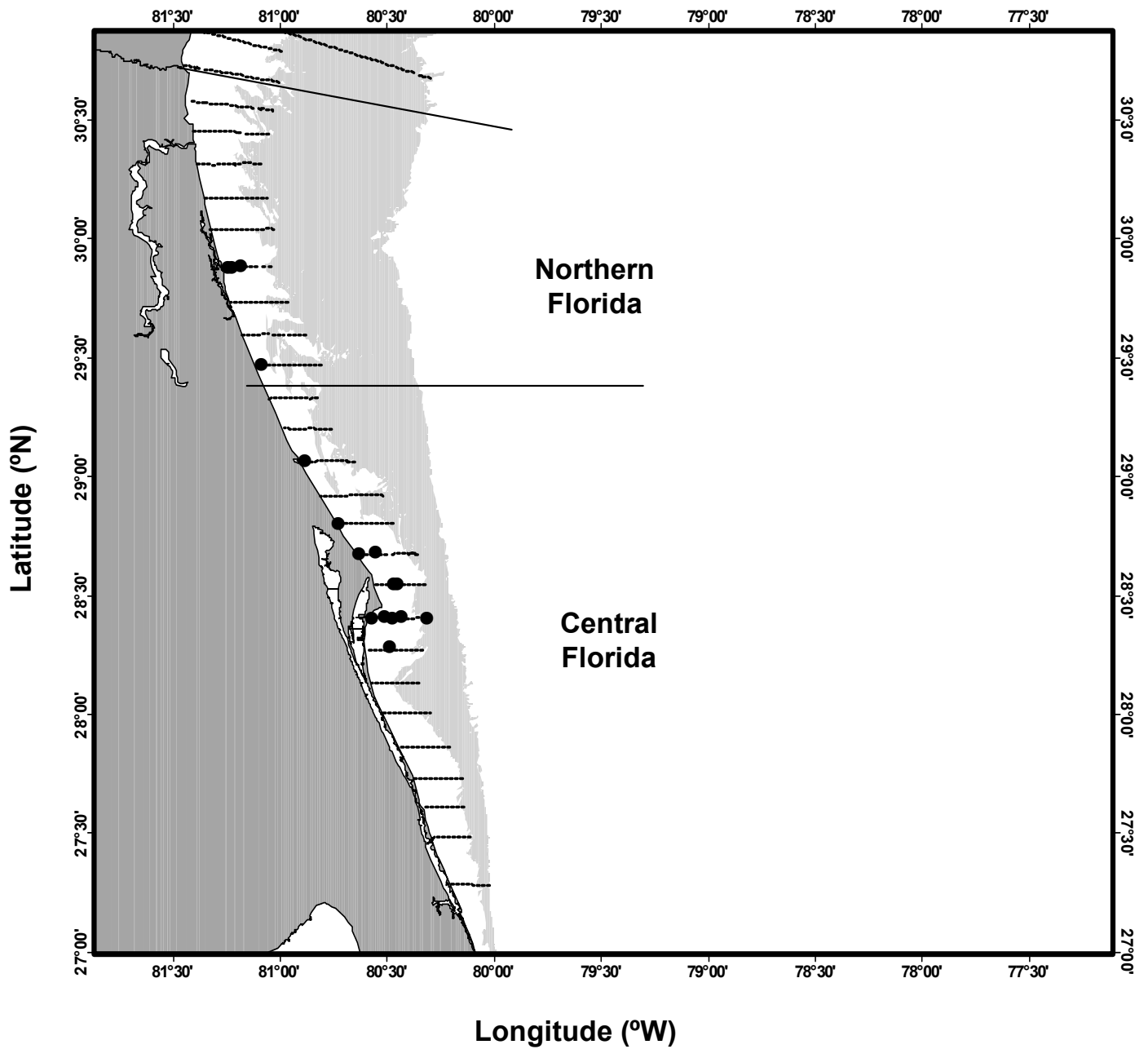
Appendix Fig. 2: Bottlenose dolphin sightings in the northern North Carolina and southern North Carolina management units during summer 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.
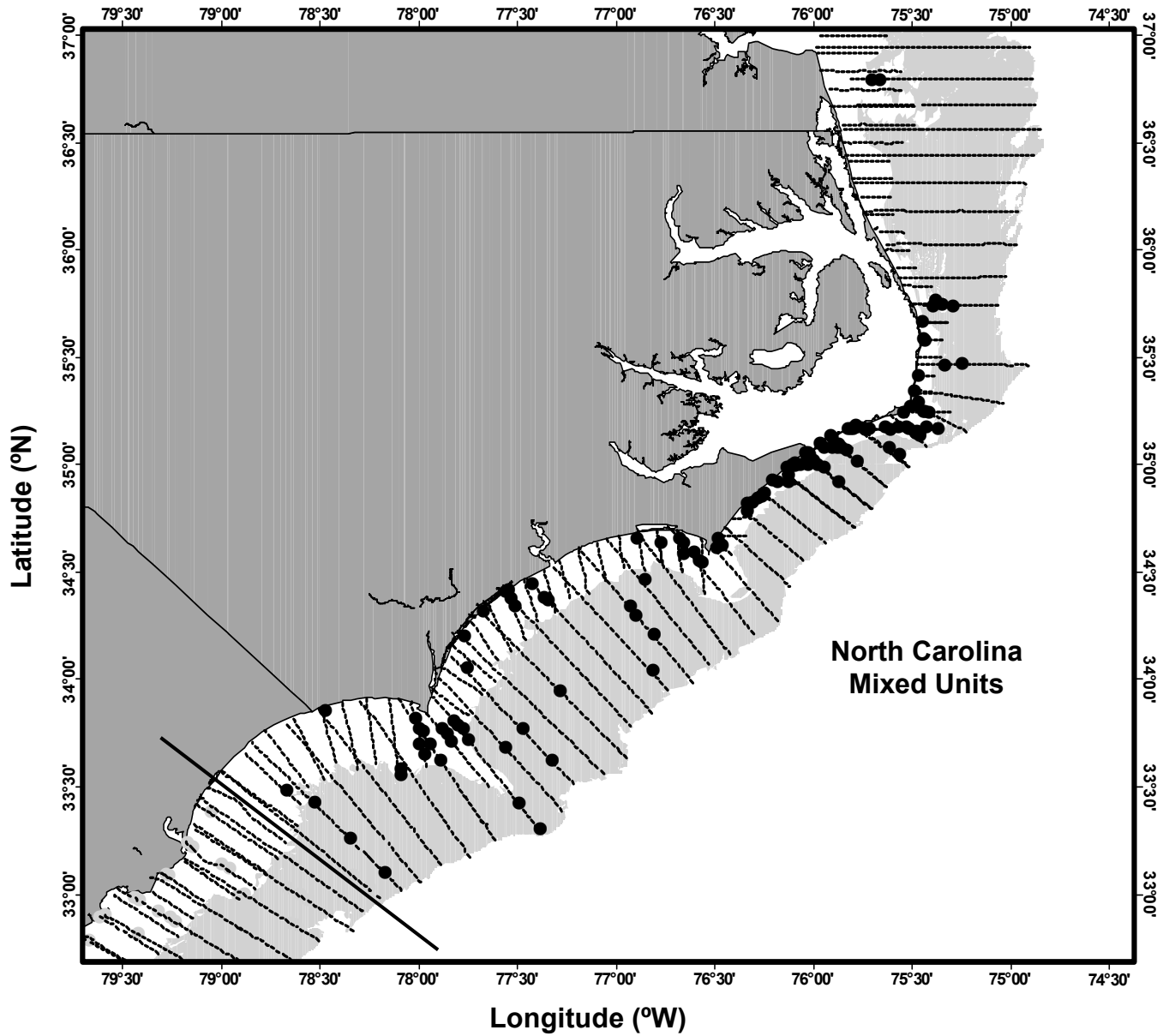
Appendix Fig. 3: Bottlenose dolphin sightings in the South Carolina and Georgia management units during summer 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.

Appendix Fig. 4: Bottlenose dolphin sightings in the northern Florida and central Florida management units during summer 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.

Appendix Fig. 5: Bottlenose dolphin sightings in the North Carolina mixed management units during winter 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.

Appendix Fig. 6: Bottlenose dolphin sightings in the South Carolina and Georgia management units during winter 2002. Shallow (0-20 m) and deep (20-40m) strata are indicated by light gray and dark gray areas respectively.